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SYSTEMATIC PLANT STUDIES

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Director, United States National Museum.

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UNITED STATES NATIONAL MUSEUM

CONTRIBUTIONS FROM THE UNITED STATES NATIONAL HERBARIUM

VOLUME 34, PART 1

DIAGNOSTIC CHARACTERISTICS OF THE FRUITS AND FLORETS OF ECONOMIC SPECIES OF NORTH AMERICAN SPOROBOLUS

By VERA LYOLA COLBRY

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DIAGNOSTIC CHARACTERISTICS OF THE FRUITS AND FLORETS OF ECONOMIC SPECIES OF NORTH AMERICAN SPOROBOLUS

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Introduction

This study is designed primarily for use in laboratories engaged in the testing of agricultural seed, where the identification of isolated seeds, fruits and florets is an integral part of the analytical procedure. Twenty of the twenty-nine species of *Sporobolus* occurring in North America are herein described. These were selected on the basis of their economic value and their possible occurrence in seed samples.

Historical consideration

With the rapid growth of seed testing within the last 30 years the need for taxonomic descriptions of seeds has been intensified, but there are relatively few detailed descriptions, keys, or illustrations available. For the most complete list to such publications the reader is referred to the annotated bibliography by Murley (1951). U. S. Agriculture Handbook 30 (1950), contains descriptions, keys, and illustrations of many of the seeds handled as agricultural crops and occurring as incidentals in them; and the Handbuch der Samenkinde, by W. Bower and A. Stählin (1955), contains descriptions and illustrations of approximately 2,500 seeds, but it has no keys and the illustrations in general do not show much diagnostic detail.

The supplementary information as to the economic value and occurrence in seed samples was obtained principally by means of questionnaires sent to the Soil Conservation Service and to seed laboratory personnel.

Information pertaining to the geographic distribution and habit was taken from A. S. Hitchcock, "Manual of the Grasses of the United States" (2 ed., revised by Agnes Chase, 1950).

The only reference found to the diagnostic characteristics of the florets and fruits of *Sporobolus* appears in U. S. Department of Agriculture Handbook 30 (1950), which consists of a short descriptive key to five species, three of which are illustrated.

Materials and methods

In order to arrive at a generalized or typical description for each species, fruits were examined from all of the mature specimens in the U. S. National Herbarium of the North American *Sporobolus* which were considered in this study.[1] In addition, bulk "seed" samples obtained from the Soil Conservation Service, U. S. Department of Agriculture, and from a few seed laboratories were studied.

The material was examined with the use of a binocular microscope largely at magnifications of 35, although certain structural details were frequently confirmed at magnifications of 45 or 60. Measurements, by means of a binocular eyepiece micrometer, were made of several fruits and florets from each specimen and averages for each species calculated. The number of individual fruits and florets measured for the various species ranged from 25 to 496, depending on the number of samples or specimens examined and the amount of variation in the material.

Acknowledgements

The writer is indebted to Dr. Lyman B. Smith for his guidance in the preparation of this paper, and to Dr. Jason R. Swallen for making available for study the plant collections at the U. S. National Herbarium, Smithsonian Institution, Washington, D. C.

The manuscript was reviewed by Dr. Oren L. Justice of the Federal Seed Laboratory, Beltsville, Md., and the fruit key was tested by seed analyst Elizabeth Fleming. Seed analysts Mildred A. Mauldin and Lou Coffey submitted supplementary fruit and floret material for study.

The following members of the staff of the Soil Conservation Service were particularly helpful in contributing fruit or plant specimens for study and for submitting information as to the economic uses of *Sporobolus:* Dr. A. A. Hanson, Dr. Jack Harlan, M. D. Atkins, Jack E. Engleman, and Joe A. Downs.

Dr. D. B. Judd, of the National Bureau of Standards, assisted in the selection and use of the Munsell Pocket Edition Constant Hue Charts from which the basic fruit colors were determined.

Structural and diagnostic characteristics

The florets of *Sporobolus* are from 1-flowered spikelets, so if free florets are found in seed samples there will be no rachilla present. The lemma and palea are membranaceous in the majority of species, although a few are found in which they are chartaceous, coriaceous, or indurate. The lemma is 1-nerved, awnless, and the palea is 2-

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[1] For a complete list of the material examined the reader is referred to the original thesis on file in the library of the George Washington University.

nerved, the keels broadly winged. In most species the palea splits between the two nerves as the fruit ripens. The fruit is free from the lemma and palea, usually falling readily from the floret at maturity. It is this characteristic that necessitates fruit descriptions.

The fruit in the grass family as a whole is commonly known as a caryopsis, since the pericarp is adherent to the seed. However, in *Sporobolus* the pericarp is loose. In all but one species herein considered the pericarp is thin and finely striate or longitudinally reticulate, slipping off easily when moist. This type of fruit is referred to as an utricle. *Sporobolus heterolepis* has a pericarp which is thick, hard and brittle, not slipping off when moist. It is designated either as an utricle or as "nutlike."

The fruit characteristics found to have diagnostic value were: Shape, size, and color of the fruit and seed; texture and surface markings of the pericarp; shape, color, and relative measurements of the scutellum and the radicle-plumule axis in relation to each other and to the endosperm; and in one species, the appearance of the area around the hilum.

The florets did not have distinctive diagnostic characteristics in all instances. It was only possible to delimit certain species or groups of species by means of floret differentiations. The diagnostic characteristics found to be of value were: texture, indumentum, length and width, general shape, shape of the lemma and palea tips, and color.

Use of keys and descriptions

Two keys were prepared. The key to the fruits is to individual species, while the key to the florets delimits certain species or groups of species. In cases where intact florets are found the latter key may ensure more rapid identification of the material. Owing to the slight differences in some of the species the fruit key is made very descriptive.

The descriptions of the species in the keys represent the most typical material studied. The full taxonomic descriptions should be used in order to identify correctly highly variable species.

Since color is an important diagnostic characteristic, an attempt was made to classify the colors of the fruits according to the Munsell color system. Munsell Pocket Edition Constant Hue Charts were used. The colors given are essentially the same as noted on the color chips with which the fruits were compared, but such terms as strong brown to designate a dark reddish brown were not used, in order to avoid confusion as to the exact shade meant. The detailed taxonomic descriptions of the fruits and florets of each species are preceded by the name and basonym, after which appears the following information in the designated order: Specimen illustrated; common

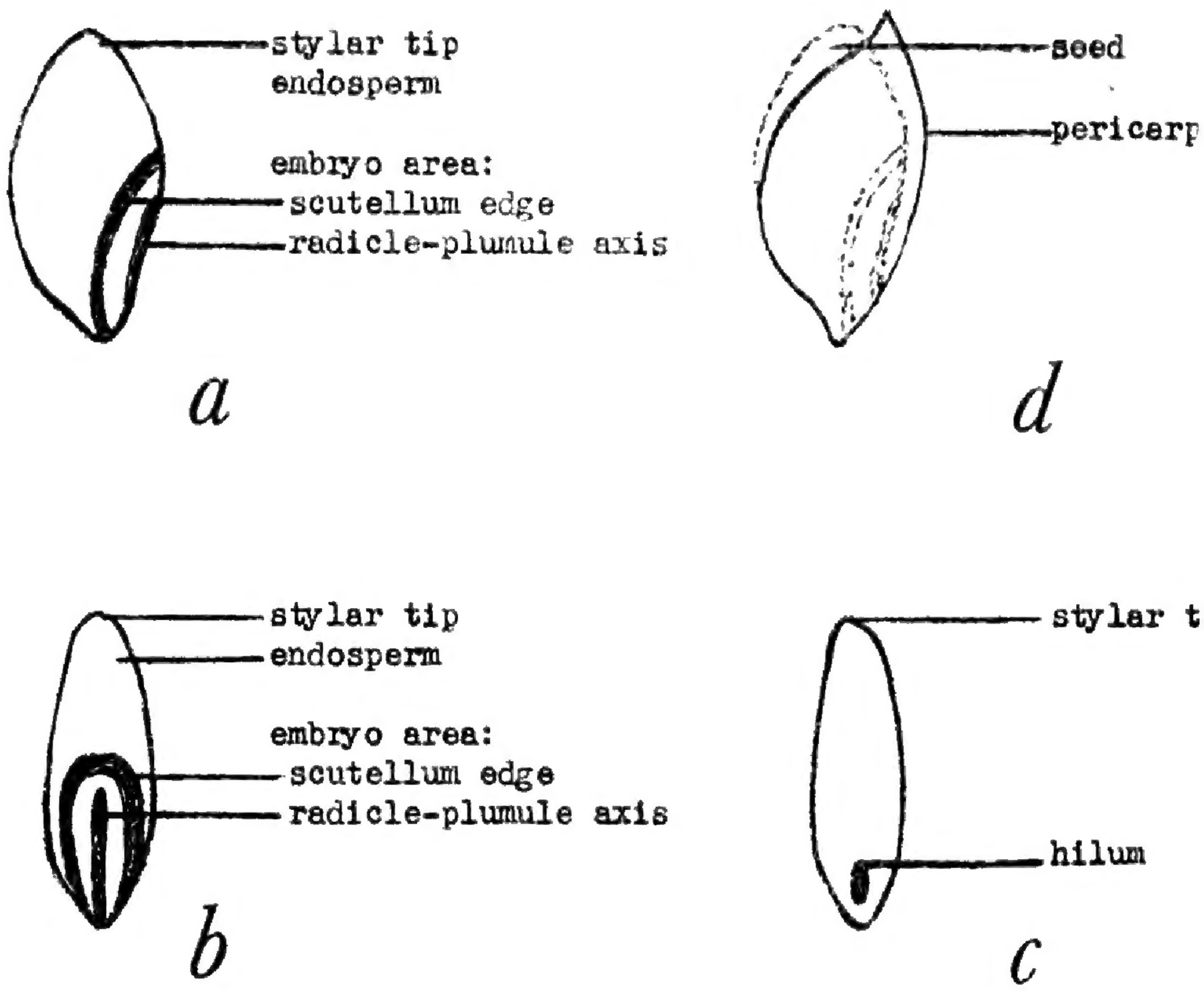


FIGURE 1.—Illustrations of terms used to designate fruit and seed morphology: *a*, Lateral view; *b*, dorsal view; *c*, ventral view; *d*, fruit with pericarp partially off.

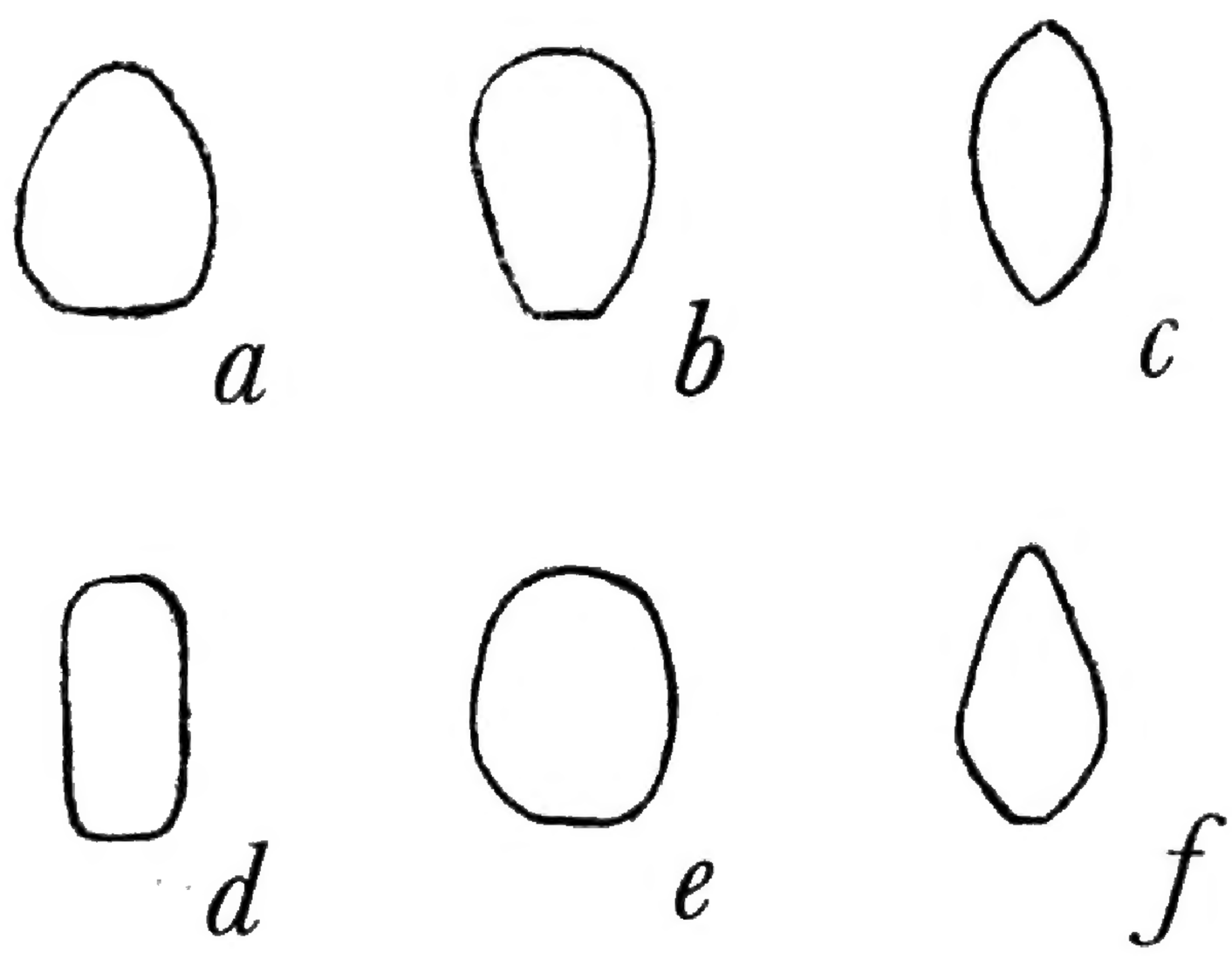


FIGURE 2.—Illustrations of terms used to designate shape: *a*, Ovoid; *b*, obovoid; *c*, ellipsoid; *d*, oblong; *d*, oval; *e*, lanceolate.

name or names; geographic distribution; habit; economic importance; and occurrence in seed samples.

The structure of *Sporobolus* fruits and florets and the terms used to designate shape in the keys and descriptions are illustrated in figures 1 and 2. In plates 1–4 are depicted the fruits and florets for each species.

The range of dimensions are given in the fruit key and both the range and median in the descriptions. The fruit measurements do not include the stylar tip and basal stipe of the pericarp.

Terminology

Certain terms as used in the keys and descriptions are defined below:

CA: approximately.
CHARTACEOUS: papery in texture.
CORIACEOUS: leathery in texture.
CUCULLATE: hood-shaped.
DORSAL: the embryo side of the fruit.
ECCENTRIC: one-sided.
EMBRYO AREA: the scutellum and the radicle-plumule axis.
INDUMENTUM: any covering, as hairiness or glandularity.
MEMBRANACEOUS: thin, like a membrane.
NARROWLY: (as applied to shape) at least twice as long as wide.
PANDURIFORM: fiddle-shaped, drawn in at the middle.
PITTED: marked with indentations or small hollows.
PLUMBEOUS: lead-colored, or greenish drab.
RETICULATE: netted.
SCABERULOUS: minutely scabrous (covered with short, stiff hairs).
STRAMINEOUS: Straw colored, or pale yellow.
STRIATE: marked by a series of fine parallel lines.
TRANSLUCENT: semitransparent; admitting passage of light but diffusing it so that objects beyond cannot be clearly distinguished.
TRANSPARENT: clear; having the property of transmitting rays of light so that objects beyond can be clearly distinguished.
VENTRAL: the hilum side of the fruit.

Taxonomic treatment

Certain species of *Sporobolus* separated only by slight inflorescence divergences were found to have equally slight fruit and floret differences. Perhaps the most difficult in which to find diagnostic characteristics for individual species occurred in the *Sporobolus cryptandrus* group. Some specimens of *S. cryptandrus* with enclosed panicles, usually occurring late in the season, are very similar to *S. contractus*. Fruit differences in color, shape, size, and to a certain extent opaqueness and flecking are fairly reliable, although a positive identification might not be possible in all cases. The only significant floret difference is size.

Sporobolus contractus and *S. giganteus* are very similar. There is a definite overlap between size and thickness of panicles, size of florets and size of fruits on some specimens. Color and shape of fruits are similar, size being the only variable. It would be impossible to identify accurately all fruits of these two species. The type specimen of *S. giganteus* (*Nash* 394) is typical for the description, having dense,

thick panicles and large fruits and florets. The type specimen of *S. cryptandrus* var. *robustus* (*Neally* 746), cited as a synonym for *S. giganteus*, has panicle, fruit, and floret measurements in the overlapping size range between *S. giganteus* and *S. contractus*.

Sporobolus flexuosus and *S. nealleyi* have definite individual fruit characteristics as well as vegetative differences in the plants. The florets cannot be distinguished in all cases.

The herbarium specimens of *Sporobolus cryptandrus* were carefully examined and measured for subspecific variation, as indicated by Jones and Fassett (1950). The overlap in the specific diagnostic characteristics is too great for positive allocation of all specimens into the subspecific categories designated by them, although there are certain broad regional differences.

Florets and fruits of the following species intergrade to some extent: *Sporobolus vaginiflorus* with *S. clandestinus*, and *S. airoides* with *S. wrightii;* the fruits have more individual diagnostic characteristics than the florets and can be distinguished in most instances. The similarity of the fruits and florets of *S. vaginiflorus* and *S. clandestinus* to each other, of interest since the former is an annual and the latter a perennial, is the only instance in which plants of unlike habit overlapped in fruit and floret characteristics. *Sporobolus airoides* and *S. wrightii* are both perennials, being separated principally by a slight inflorescence divergence.

While the plants of *Sporobolus vaginiflorus* and *S. neglectus* are very similar, their identification by fruit and floret characteristics was found to be very dependable. The fruits of the latter are variously mottled while those of the former are not, and there are also differences in size and shape. The florets of *S. neglectus* are chartaceous and glabrous while those of *S. vaginiflorus* are coriaceous or indurate (except for very occasional cleistogamous florets) and usually sparingly pubescent.

The published descriptions of the florets of *S. vaginiflorus* do not cover the range of characteristics for the species. The florets are described as sparsely pubescent, sometimes mottled with dark spots. Statements as to the texture of the lemma and palea are not complete. Examination of the National Herbarium specimens revealed that the indumentum of the florets varied from sparsely pubescent to shiny, microscopical, conical glands. This latter type of floret always has a palea which is split between the two nerves, the split so complete as to cause the palea to appear double. The florets are indurate and mottled, with plump, abruptly acute to incurved or cucullate lemma and palea. Specimens with this kind of floret occur in the limestone areas of Arkansas and Missouri. There is a gradual intergrading of this type with the narrower, thinner textured, slightly pubescent floret

occurring in other regions. It was thought that perhaps the characteristic of the palea splitting between the two nerves might be of some significance, but it could not be correlated with any other constant variable in the florets or fruits. In general, specimens from the northeastern and eastern states have paleas that do not split at fruit maturity. Those from the central, south, and southwestern states have either split or nonsplit paleas.

The form of *Sporobolus neglectus* from the Ozark mountains, designated by Fernald (1933) as *S. ozarkanus*, has florets and fruits like the other forms of *S. neglectus* examined. The type which he described as *S. vaginiflorus* var. *inaequalis* intergrades with florets and fruits of *S. vaginiflorus* from other areas.

The varieties of *Sporobolus asper* were not studied due to lack of available mature fruit material.

Sporobolus patens was not included, as only one specimen was available for study. This species has a limited distribution in the United States, being reported only from southern Arizona. The fruits are so similar to those of *S. pulvinatus* that it is doubtful whether these two species can be distinguished.

Key to fruits

A. Pericarp thick, hard, brittle and opaque; fruits subglobose, ca. 1.0–2.0 mm. in diameter . . . . . **1. S. heterolepis** (pl. 1,A)

A. Pericarp thin, mucilaginous when wet, hyaline; striate or reticulate.

B. Embryo as long as seed to slightly shorter; fruits narrowly eccentric obovoid, plump, tapering to base; length 2.1–3.0 mm., width 1.0–1.5 mm. **2. S. interruptus** (pl. 1,B)

B. Embryo not more than ¾ length of seed.

C. Fruits eccentric ovoid, translucent; seeds smooth, not microscopically pitted; pericarp extremely finely striate, scarcely evident.

D. Fruits bulging dorsally above embryo tip; endosperm light yellowish brown or dark orange-brown.

E. Embryo usually less than ½ length of seed; fruits narrowly ovoid; endosperm usually faintly reddish flecked; scutellum brown or reddish; length 2.2–3.6 mm., width 0.6–1.3 mm., thickness 0.4–1.0 mm . . . . . **3. S. clandestinus** (pl. 1,C)

E. Embryo usually more than ½ length of seed (often ¾); fruits narrowly or broadly ovoid; endosperm rarely reddish flecked; scutellum brown, reddish, or blackish; length 1.0–3.0 mm., width 0.4–1.5 mm., thickness 0.3–1.4 mm. **4. S. vaginiflorus** (pl. 1,D)

D. Fruits bulging ventrally toward base; narrowly ovoid; endosperm light yellowish brown or yellowish orange; embryo area reddish brown; length 1.0–1.5 mm., width 0.4–0.7 mm., thickness 0.2–0.5 mm . . . . . **5. S. texanus** (pl. 1,E)

C. Fruits rarely eccentric ovoid (if so, not translucent); seeds either microscopically pitted or pericarp evidently striate or reticulate.

F. Fruits dark shades of red, orange, or brown, or fruits gray, dark reddish brown flecked or mottled; pericarp frequently dark red or black striate.

G. Scutellum edge prominent, dark red or black at seed maturity.

H. Fruits tapering to thin edges dorsally and ventrally, strongly flattened laterally, broad.

I. Fruits ellipsoid; endosperm orange or reddish brown; translucent at maturity; length 1.7–2.6 mm., width 0.8–1.2 mm., thickness 0.4–0.6 mm . . . . **6. S. purpurascens** (pl. 1,F)

I. Fruits broadly obovoid or broadly ovoid; endosperm reddish or reddish brown; opaque or semitranslucent; length 1.5–1.8 mm., width 1.0–1.2 mm., thickness 0.4–0.7 mm.
7. S. junceus (pl. 2,A)

H. Fruits not tapering to thin edges dorsally and ventrally.

J. Embryo ¾ length of seed; seeds reddish brown mottled; endosperm usually grayish and semitranslucent; shape suboval or suboblong, plump.

K. Fruits in dorsal view sharply keeled above embryo tip; scutellum edge narrow (ca. 0.1 mm.); radicle-plumule axis broad, twisted; length 0.8–2.5 mm., width 0.4–1.0 mm., thickness 0.3–0.7 mm . . **8. S. neglectus** (pl. 2,B)

K. Fruits in dorsal view convex the entire length; scutellum edge broad (ca. 0.2–0.3 mm.); radicle-plumule axis narrow, almost straight; length 1.1–2.0 mm., width 0.6–1.3 mm., thickness 0.5–1.1 mm . . . . . **9. S. asper** (pl. 2,C)

J. Embryo less than ¾ length of seed; seeds not mottled; endosperm reddish or yellowish orange; shape suboblong, usually strongly compressed laterally; pericarp dark reddish striate, highly mucilaginous at seed maturity, and then frequently forming a dark rim on the edges of the fruits; length 0.8–1.4 mm., width 0.5–0.8 mm., thickness 0.2–0.4 mm . . . . . **10. S. poiretii** (pl. 2,D)

G. Scutellum edge not prominent, about same color as endosperm; pericarp strongly dark red or black striate; fruits plump, length 0.9–1.7 mm., width 0.4–0.9 mm.

L. Stylar tip rounded; fruits suboblong or suboval, dark yellowish brown or light brown; seeds rarely reddish flecked; thickness 0.4–0.7 mm . . . . . **11. S. airoides** (pl. 2,E)

L. Stylar tip usually pointed and strongly laterally compressed; fruits predominantly ovoid, dark reddish brown (occasionally light brown); seeds usually reddish flecked; thickness 0.3–0.7 mm . . . . . **12. S. wrightii** (pl. 2,F)

F. Fruits light shades of red, orange, brown, or gray, never dark reddish brown mottled; pericarp never dark red or black striate, but frequently light red, rusty, or purplish striate.

M. Fruits flattish at base, embryo without a prominent overhang; hilum within a basally prominent black half-rim; fruits suboval or broadly ovoid; uniformly light reddish orange; endosperm faintly light reddish flecked; length 0.7–1.0 mm., width 0.3–0.7 mm . . . . . **13. S. buckleyi** (pl. 3,A)

M. Fruits pointed at base, embryo with a prominent overhang; hilum not within a basally prominent black half-rim.

N. Scutellum in dorsal view pandurate; in lateral view of fruits, inner scutellum reflected in a broad, dark semicircle through the endosperm; radicle-plumule axis broad.

O. Embryo area greenish black; fruits light yellowish gray or yellowish orange; obovoid; length 0.8–1.0 mm., width 0.4–0.7 mm., thickness 0.2–0.5 mm . . **14. S. pulvinatus** (pl. 3,B)

O. Embryo area dark reddish brown; fruits light orange reddish; obovoid, suboval or subelliptic; length 0.7–1.0 mm., width 0.4–0.6 mm., thickness 0.2–0.4 mm.

15. S. pyramidatus (pl. 3,C)

N. Scutellum in dorsal view oval; in lateral view of fruit, inner scutellum either not reflected or narrowly and unevenly reflected through the endosperm; radicle-plumule axis narrow.

P. Fruits extremely light yellowish brown or pale orange-yellow, sometimes almost white; endosperm not rusty or light reddish flecked but usually internally "starchy" or granularly mottled.

Q. Fruits not strongly flattened laterally; average length less than 1.0 mm.; pericarp frequently purplish striate, sometimes rusty striate.

R. Fruits broadly obovoid, frequently "pinched" laterally toward the center; embryo area rusty or light reddish brown; length 0.7–0.9 mm., width 0.5–0.8 mm.

16. S. flexuosus (pl. 3,D)

R. Fruits narrowly ovoid, not "pinched" laterally toward the center; embryo area rusty or purplish brown; length 0.7–1.0 mm., width 0.3–0.5 mm.

17. S. nealleyi (pl. 3,E)

Q. Fruits strongly laterally flattened; average length over 1.0 mm.; pericarp not purple striate, but sometimes rusty striate; fruits broadly elliptic or broadly ovoid.

S. Fruit length 0.8–1.2 mm., width 0.4–0.8 mm.

18. S. contractus (pl. 3,F)

S. Fruit length 1.0–1.9 mm., width 0.6–0.9 mm.

19. S. giganteus (pl. 4,A)

P. Fruits darker: moderate orange, brownish orange or light reddish brown; endosperm faintly rusty or light reddish flecked, rarely internally "starchy" or granularly mottled; fruits laterally flattened at stylar tip; ovoid or obovoid; pericarp sometimes rusty or light reddish striate; length 0.6–1.3 mm., width 0.3–0.8 mm . . **20. S. cryptandrus** (pl. 4,B)

Key to florets

A. Florets coriaceous, indurate, or chartaceous.

B. Florets coriaceous or indurate; pubescent or microscopically striate with shiny conical glands; opaque; color gray, tan, or purplish, unevenly splotched with black, purple, or green.

C. Florets 4.5–13.0 mm. long; palea 0.5–6.0 mm. longer than the lemma; palea acuminate (rarely acute), not split between the two nerves; lemma acute or acuminate . . . . . **3. S. clandestinus** (pl. 1,C)

C. Florets 1.6–7.0 mm. long; palea subequal to 2.0 mm. longer than lemma;

lemma and palea acuminate, acute or incurved or cucullate; palea sometimes split between the two nerves . . **4. S. vaginiflorus** (pl. 1,D)

B. Florets chartaceous; glabrous; smooth; opaque or semiopaque; color white, greenish or purplish tinged, or purplish; length 1.1–3.0 mm.
8. S. neglectus (pl. 2,B)

A. Florets membranaceous; essentially glabrous (some species sparingly microscopically scaberulous); opaque, semiopaque, or transparent.

D. Length of florets 3.0 mm. or over.

E. Florets 1.0 mm. thick or over.

F. Lemma and palea acute; florets ca. 1.1 mm. thick, 1.1 mm. wide, and 6.0 mm. long. . . . . **2. S. interruptus** (pl. 1,B)

F. Lemma and palea subacute; florets distended by the globose fruits; ca. 2.0 mm. thick, 2.0 mm. wide, and 4.0 mm. long.
1. S. heterolepis (pl. 1,A)

E. Florets less than 1.0 mm. thick (*S. asper* occasionally 1.1 mm. thick).

G. Florets bronze; 3.0–4.0 mm. long and ca. 1.0 mm. wide; lemma acute; fruits often sticking to the edges of the palea.

H. Palea acute. . . . . **6. S. purpurascens** (pl. 1,F)

H. Palea obtuse or subacute. . . . . **7. S. junceus** (pl. 2,A)

G. Florets not bronze.

I. Floret length 4.0–7.0 mm., two to three times as long as the fruit; lemma and palea subacute; color pale yellowish gray, light green or purplish tinged. . . . . **9. S. asper** (pl. 2,C)

I. Floret length 2.2–3.5 mm., not more than twice as long as the fruit; lemma and palea acute or acuminate; color stramineous or plumbeous. . . . . **19. S. giganteus** (pl. 4,A)

D. Length of florets under 3.0 mm.

J. Florets bronze tinged. . . . . **11. S. airoides** (pl. 2,E)
12. S. wrightii (pl. 2,F)

J. Florets not bronze tinged.

K. Palea obtuse, usually erose and dentate; lemma acute (sometimes subobtuse).

L. Florets frequently smutted; fruits usually sticking to the outside or tips of the florets; length 1.5–2.0 mm.
10. S. poiretii (pl. 2,D)

L. Florets not smutted; length ca. 1.0–2.0 mm.
13. S. buckleyi (pl. 3,A)
14. S. pulvinatus (pl. 3,B)
15. S. pyramidatus (pl. 3,C)

K. Palea acute; lemma acute.

M. Florets usually opaque or semiopaque.

N. Floret length 2.1–2.7 mm.; fruits frequently sticking to the outside or tips of the florets. . . . . **5. S. texanus** (pl. 1,E)

N. Floret length 1.5–2.0 mm.; florets usually dark purplish tinged.
17. S. nealleyi (pl. 3,E)

M. Florets usually transparent or semiopaque (rarely opaque).

O. Floret length (1.4)–1.8–(2.0) mm. . . **20. S. cryptandrus** (pl. 4,B)

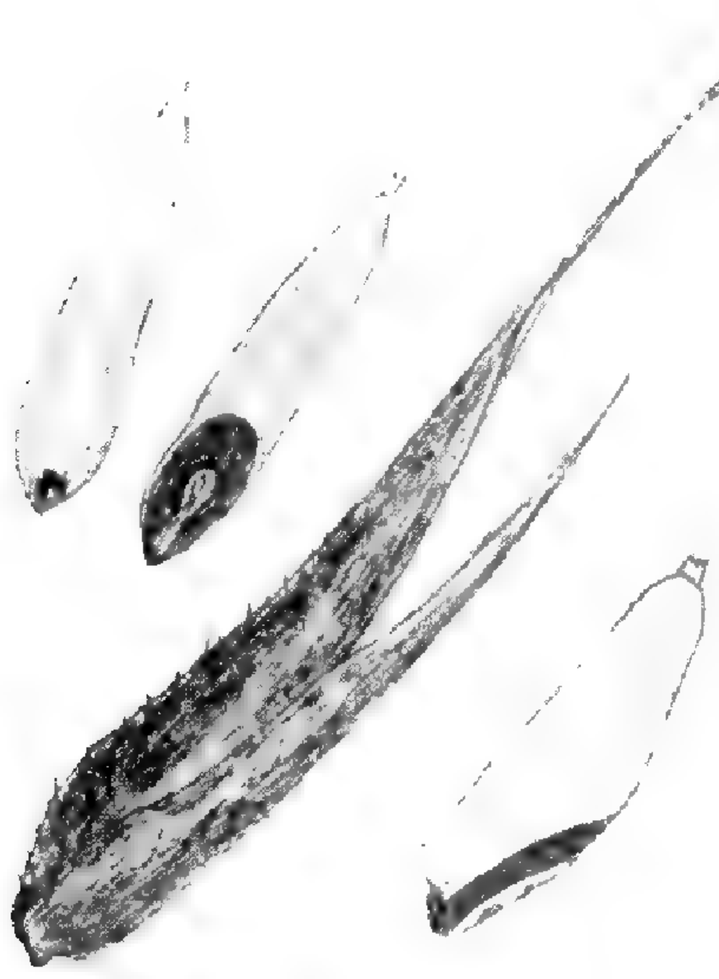
O. Floret length (1.5)–2.1–(2.7) mm. . . **16. S. flexuosus** (pl. 3,D)

O. Floret length (1.5)–2.4–(2.9) mm. . . **18. S. contractus** (pl. 3,F)

O. Floret length (2.2)–2.9–(3.5) mm. . . **19. S. giganteus** (pl. 4,A)

A, *S. heterolepis*, X 6.3

B, *S. interruptus*, X 6.3



C, *S. clandestinus*, X 6.3

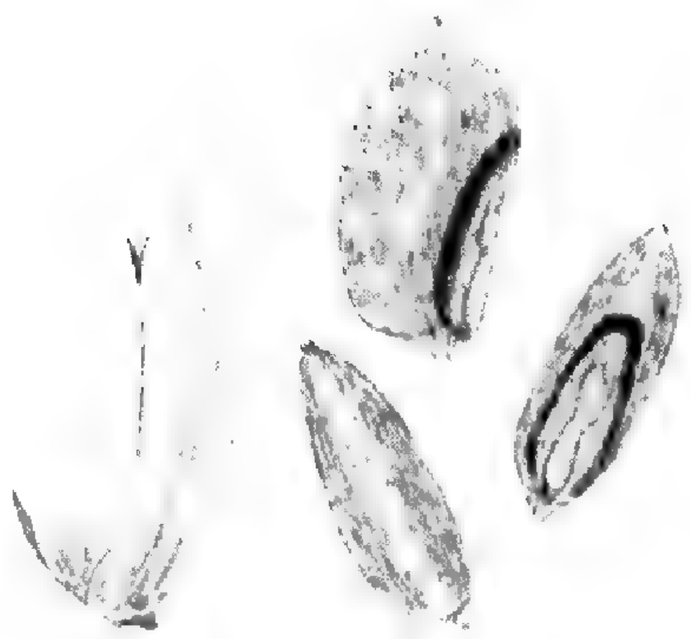
D, *S. vaginiflorus*, X 6.3

E, *S. texanus*, X 11.3

F, *S. purpurascens*, X 9.4

SPOROBOLUS FRUITS, SEEDS, AND FLORETS.

A, *S. junceus*, X 9.4

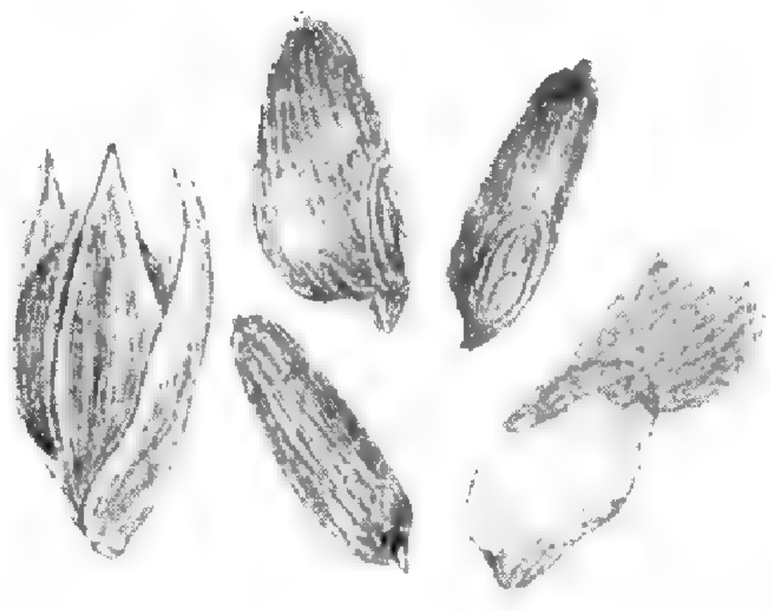


B, *S. neglectus*, X 10.7

C, *S. asper*, X 10.7

D, *S. poiretti*, X 11.3

E, *S. airoides*, X 11.3



F, *S. wrightii*, X 11.3

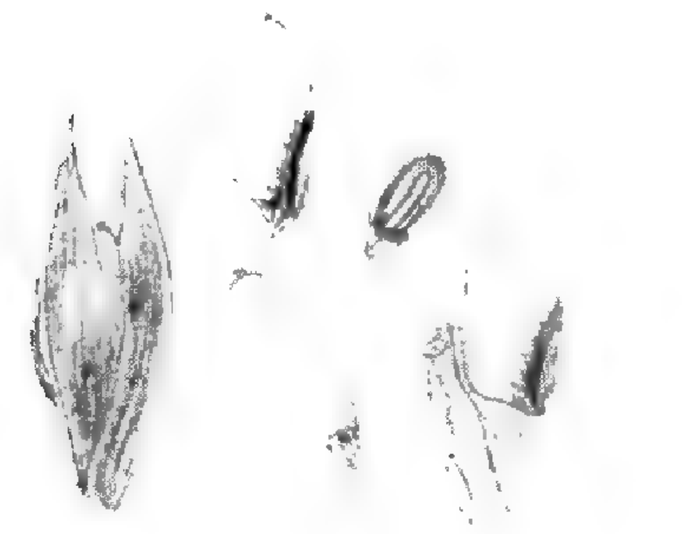
SPOROBOLUS FRUITS, SEEDS, AND FLORETS.

A, *S. buckleyi*, X 11.3

B, *S. pulvinatus*, X 11.3

C, *S. pyramidatus*, X 11.3

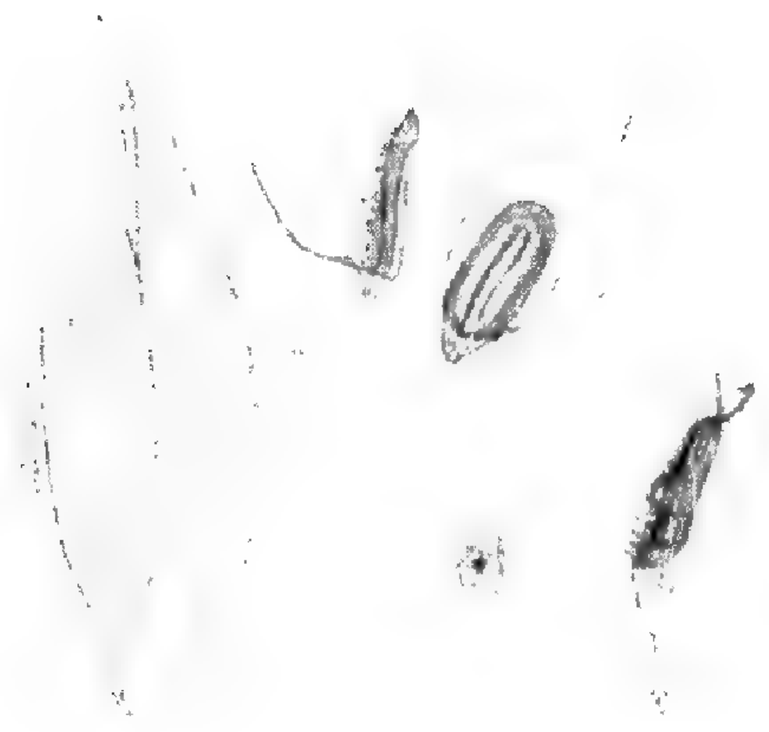
D, *S. flexuosus*, X 11.3



E, *S. nealleyi*, X 11.3

F, *S. contractus*, X 11.3

SPOROBOLUS FRUITS, SEEDS, AND FLORETS.



A, *S. giganteus*, X 11.3

B, *S. cryptandrus*, X 11.3

SPOROBOLUS FRUITS SEEDS, AND FLORETS.

Descriptions

1. **Sporobolus heterolepis** (A. Gray) A. Gray, Man. 567. 1848. Based on *Vilfa heterolepis* A. Gray.
Vilfa heterolepis A. Gray, Ann. Lyc. N.Y. 3:233. 1835. Watertown, New York, *Crawe*.

PLATE 1, A

Fruits: Length, width and thickness ca. the same: (1.0)–1.5–(2.0) mm.; opaque; shape subglobose, eccentric in lateral view; color grayish yellow, frequently greenish gray or purplish splotched; pericarp thick, brittle, indehiscent and minutely longitudinally reticulate.

Seeds: These were removed from the pericarp with extreme difficulty. Although reported as being free from the pericarp, they are partially adherent at the stylar tip.

Length, width, and thickness ca. the same as for the fruits; opaque; longitudinally blackish or reddish striate or reticulate, and glandular shiny; shape irregularly obovoid or skull-like, flattened dorsally; color of endosperm variable (yellow, yellowish gray, light brown, grayish greenish yellow, or grayish reddish brown); embryo strikingly darker, sometimes almost black; embryo large, prominent, almost completely covering the dorsal side of the seed; scutellum very broad; radicle-plumule axis short and narrow.

Florets: Length (3.0)–4.0–(4.9) mm.; width and thickness ca. the same as for the fruits; membranaceous; glabrous; color plumbeous or stramineous, frequently purplish or greenish tinged; palea slightly longer and wider than the lemma; nerves of the lemma and palea glabrous or slightly scaberulous toward the tips; palea at fruit maturity splits completely between the 2 nerves, the 2 apices subacute; lemma subacute, at maturity distended at the base by the subglobose fruit.

Specimen illustrated: *C. O. Johnston*, December 1920, in meadow, Manhattan, Kansas.

Common name: Prairie dropseed.

Geographic distribution: Quebec to Saskatchewan, south to Connecticut, eastern Texas, and Colorado; prairies.

Habit: Perennial, in dense tufts.

Economic importance: A true prairie species, disappearing under moderate to heavy grazing; common in hay meadows; common in eastern Kansas, but seed has never been produced or collected in quantity for seeding.

Occurrence in seed samples: Not reported.

2. Sporobolus interruptus Vasey, Bull. Torrey Bot. Club 15:8. 1888. Arizona, *Coues* and *Palmer* 66 in 1886; San Francisco Forest, *Rusby* 15 in 1883 (the Rusby specimen, distributed as No. 885, the type). PLATE 1,B

Fruits: Length (2.1)–2.6–(3.0) mm.; width (1.0)–1.1–(1.5) mm.; thickness (1.0)–1.1–(1.3) mm.; opaque or semitranslucent; shape narrowly eccentric obovoid; convex ventrally, plump, tapering to the base; embryo large, prominent, almost completely covering the dorsal side of the seed; color of endosperm yellowish reddish brown, grayish tinged; embryo darker; pericarp brownish black striate or reticulate, the ridges and interspaces grayish mucilaginous.

Florets: Length ca. 6.0 mm.; width and thickness ca. the same as for the fruits; opaque; membranaceous; glabrous; color plumbeous or stramineous; lemma and palea about the same length, the tips acute; nerves of palea glabrous; nerve of lemma glabrous to minutely scaberulous toward the tip; palea splits at fruit maturity.

Specimen illustrated: *Joe A. Downs* 951, Soil Conservation Service "seed" sample, Arizona.

Common name: Black dropseed.

Geographic distribution: Arizona, grassy plains and hills.

Habit: Perennial, densely tufted.

Economic importance: Good forage grass, but doubtful if it will ever be used in revegetation.

Occurrence in seed samples: Not reported.

3. Sporobolus clandestinus (Biehler) Hitchc., Contr. U. S. Nat. Herb. 12:150. 1908. Based on *Agrostis clandestina* Biehler. PLATE 1,C

Agrostis clandestina Biehler, Pl. Nov. Herb. Spreng. Cont. 8. 1807. Pennsylvania, *Muhlenberg.*

Fruits: Length (2.2)–2.9–(3.6) mm.; width (0.6)–0.9–(1.3) mm.; thickness (0.4)–0.6–(1.0) mm.; translucent; shape narrowly eccentric ovoid, bulging dorsally above the embryo tip; embryo usually less than ½ the length of the seed; color of endosperm and radicle-plumule axis light yellowish brown or dark orange brown; endosperm usually faintly reddish flecked; scutellum edge broad, flat, bandlike, darker than the endosperm and the radicle-plumule axis; pericarp almost smooth, sometimes faintly reddish striate.

Florets: Length (4.5)–7.2–(13.0) mm.; width and thickness ca. the same as for the fruits; opaque; coriaceous; sparingly long-pubescent; microscopically striate with shiny conical glands; color gray, tan, or purplish, unevenly splotched with black, purple, or green; palea (0.5)–1.6–(6.0) mm. longer than the lemma; lemma acute or acuminate; palea usually acuminate, rarely acute; palea does not split at fruit maturity.

Specimen illustrated: *Jason R. Swallen* 5625; Nov. 16, 1938; dry sandy ground east of Gainesville, Florida.

Common name: Hidden dropseed.

Geographic distribution: Connecticut to Wisconsin and Kansas, south to Florida and Texas; sandy fields, pine barrens, hills and prairies.

Habit: Perennial.

Economic importance: Palatable; especially valuable in winter when stock seem to prefer it to other warm-season grasses.

Occurrence in seed samples: Reported in native grass and legume seed samples, in samples of *S. cryptandrus*, and in lespedeza (*Lespedeza* spp.) samples.

4. Sporobolus vaginiflorus (Torr.) Wood, Class-book ed. 1861. 775. 1861.
Based on *Vilfa vaginiflora* Torr. PLATE 1,D
Vilfa vaginiflora Torr. ex. Gray, N. Amer. Gram. and Cyp. 1: No. 3. 1834; Trin., Mém. Acad. St. Pétersb. VI. Sci. Nat. 4¹:56. 1840. New Jersey.

Fruits: Length (1.0)–2.0–(3.0) mm.; width (0.4)–0.7–(1.5) mm.; thickness (0.3)–0.5–(1.4) mm.; translucent; shape narrowly or broadly eccentric ovoid, bulging dorsally above the embryo tip; embryo usually more than half length of seed, frequently three-quarters; color of endosperm and radicle-plumule axis light yellowish brown or dark orange brown; endosperm rarely reddish flecked; scutellum edge broad, flat, bandlike, at full maturity strikingly darker than the endosperm and the radicle-plumule axis (sometimes almost black); pericarp almost smooth, rarely faintly reddish striate.

Florets: Length (1.6)–3.3–(7.0) mm.; width and thickness ca. the same as for the fruits; opaque; coriaceous or indurate; usually sparingly pubescent; microscopically striate with shiny, conical glands (6 specimens observed in which the indumentum consisted of these shiny, conical glands alone); color gray, tan or purplish, unevenly splotched with black, purple, or green; length of palea in relation to the lemma variable, but never more than 2.0 mm. longer than the lemma; lemma and palea tips acuminate, acute or incurved to cucullate; palea usually does not split at fruit maturity (only 10 specimens were observed with split paleas); cleistogamous florets like the others or rarely membranaceous, whitish.

Specimen illustrated: *Vera L. Colbry* 17; Oct. 24, 1954; low clay ground, near stream; Prince Georges County, Maryland.

Common name: Poverty dropseed.

Geographic distribution: Maine and Ontario to Minnesota and Nebraska, south to Georgia, Texas, and Arizona; sandy soil or open waste ground.

Habit: Annual.

Economic importance: Considered a weed; no value except for erosion control when it invades abandoned fields.

Occurrence in seed samples: Has been found in native grass and legume seed samples, in *S. cryptandrus* samples, and in lespedeza (*Lespedeza* spp.) samples from the southeastern states.

5. Sporobolus texanus Vasey, Contr. U. S. Nat. Herb. 1:57. 1890. Screw Bean, Presidio County, Texas, *Nealley* (755). PLATE 1,E

Fruits: Length (1.0)–1.3–(1.5) mm.; width (0.4)–0.5–(0.7) mm.; thickness (0.2)–0.4–(0.5) mm.; translucent; shape narrowly eccentric ovoid, bulging ventrally toward the base; color of endosperm light yellowish brown or yellowish orange; embryo area reddish brown; scutellum edge narrow, the inner part slightly sunken around the elevated, twisted radicle-plumule axis; pericarp very finely striate or reticulate, frequently partially slipped off mature fruits, causing them to adhere to the florets.

Florets: Length (2.1)–2.3–(2.7) mm.; width and thickness ca. the same as for the fruits; opaque or semiopaque; membranaceous; essentially glabrous, sometimes sparingly scaberulous toward the tips; color plumbeous or stramineous, frequently greenish or purplish tinged; palea slightly shorter than the lemma; lemma and palea tips acute, the nerves minutely scaberulous toward the tips; palea splits at fruit maturity; fruits with the pericarp partially slipped off frequently adhering to the tips or sides of the florets.

Specimen illustrated: *S. M. Tracy* 8197; Oct. 6, 1902; Carlsbad, New Mexico.

Common name: Texas dropseed.

Geographic distribution: Kansas and Colorado to Texas and Arizona; mesas, valleys, and salt marshes.

Habit: Perennial, in close, hemispherical tufts.

Economic importance: Palatable, but no place in a seeding program; one of the first grasses to come into alkaline flats in river bottom succession; eventually crowded out by climax forms.

Occurrence in seed samples: Not reported.

6. Sporobolus purpurascens (Swartz) Hamilt., Prodr. Pl. Ind. Occ. 5. 1825. Based on *Agrostis purpurascens* Swartz. PLATE 1,F

Agrostis purpurascens Swartz, Prodr. Veg. Ind. Occ. 25. 1788. Jamaica, *Swartz.*

Fruits: Length (1.7)–2.1–(2.6) mm.; width (0.8)–1.0–(1.2) mm.; thickness (0.4)–0.5–(0.6) mm.; translucent at maturity; shape ellipsoid; strongly laterally flattened; convex laterally, and tapering to thin, sharp edges dorsally and ventrally; slightly bulging ventrally and laterally toward the base; color of endosperm orange or reddish brown; scutellum edge broad (ca. 0.2 mm. wide toward the lower edge and 0.1 mm. wide at the upper edge), the outer rim elevated; scutellum dark, black at full seed maturity; radicle-plumule axis elevated and strongly keeled, the same color as the endosperm; pericarp dull,

minutely striate, the striations often reddish; pericarp readily slipping off mature fruits.

Florets: Length 3.0 to 4.0 mm.; width and thickness ca. the same as the fruits; palea transparent; lemma semiopaque, membranaceous, glabrous; color bronze, sometimes purplish tinged; lemma and palea tips acute, usually spread apart at the tips, exposing the fruits; palea splits at fruit maturity; fruits with the pericarp partially slipped off often sticking to the lemma and palea.

Specimen illustrated: *C. L. Lundell & Amelia A. Lundell* 8846; May 10, 1940; in sand along railroad; live-oak belt; north of Encino, Brooks County, Texas.

Common name: Purple dropseed.

Geographic distribution: Southern Texas and eastern Mexico; West Indies to Brazil; sandy prairies.

Habit: Perennial, in dense bunches.

Economic importance: Not reported.

Occurrence in seed samples: Not reported.

7. Sporobolus junceus (Michx.) Kunth, Rév. Gram. 1:68. 1829. Based on *Agrostis juncea* Michx. PLATE 2,A

Agrostis juncea Michx. Fl. Bor. Amer. 1:52. 1803, not *A. juncea* Lam., 1783. Carolina, *Michaux.*

Fruits: Length (1.5)–1.7–(1.8) mm.; width (1.0)–1.0–(1.2) mm.; thickness (0.4)–1.6–(0.7) mm.; opaque or semitranslucent; shape broadly obovoid or broadly ovoid; strongly laterally flattened; convex laterally and tapering to fairly thin edges dorsally and ventrally; slightly bulging ventrally and laterally toward the base; color of endosperm reddish or reddish brown; scutellum, radicle-plumule axis and pericarp the same as for *S. purpurascens*.

Florets: Palea tips obtuse or subacute; otherwise the same as for *S. purpurascens*.

Specimen illustrated: *Albert Ruth* 91; July 1898; dry sandy soil, Lookout Mountain; DeSoto Falls, Alabama.

Common name: Pineywoods dropseed.

Habit: Perennial, in dense bunches.

Economic importance: Not reported.

Occurrence in seed samples: Not reported.

8. Sporobolus neglectus Nash, Bull. Torrey Bot. Club 22:464. 1895. Massachusetts to Kentucky, Tennessee, and Kansas (type, Woodruff Gap, New Jersey, *Britton* in 1887). PLATE 2,B

Fruits: Length (0.8)–1.4–(2.5) mm.; width (0.4)–0.7–(1.0) mm.; thickness (0.3)–0.5–(0.7) mm.; semitranslucent; shape suboval or suboblong; plump; keeled dorsally above the embryo tip; compressed laterally toward the stylar tip; in ventral and dorsal views lanceolate; embryo three-quarters length of seed; color of endosperm

grayish yellowish brown or brownish orange; endosperm strongly reddish brown mottled and usually pitted; scutellum edge narrow (ca. 0.1 mm. broad), bandlike, at full maturity almost black; radicle-plumule axis broad, elevated, twisted, and lighter in color than the scutellum edge; pericarp finely striate.

Florets: Length (1.1)–2.2–(3.0) mm.; width and thickness slightly more than for the fruits; opaque or semiopaque; chartaceous; glabrous; color white, variously greenish or purplish streaked, or purplish; florets wide toward the center; lemma and palea tips acute (palea frequently abruptly acute); palea glabrous on the nerves; lemma scaberulous on the nerve near the tip; palea splits at fruit maturity.

Specimen illustrated: *H. L. Bolley* 867; Aug. 27, 1891; Fargo, North Dakota.

Common name: Puffsheath dropseed.

Geographic distribution: Quebec and Maine to Montana, south to Virginia, Tennessee, and Texas; also Washington and Arizona; dry open ground and sandy fields.

Habit: Annual.

Economic importance: No value except for erosion control when it invades abandoned fields or other bare areas.

Occurrence in seed samples: Reported as occurring in native grass and legume samples and in *S. cryptandrus* samples.

9. Sporobolus asper (Michx.) Kunth, Rév. Gram. 1:68. 1829. Based on PLATE 2,C

Agrostis aspera Michx.

Agrostis aspera Michx., Fl. Bor. Amer. 1:52. 1803. Illinois, *Michaux.*

Fruits: Length (1.1)–1.6–(2.0) mm.; width (0.6)–1.0–(1.3) mm; thickness (0.5)–0.8–(1.1) mm.; semitranslucent; shape suboval or suboblong; plump; in dorsal view convex the entire length, in ventral and dorsal views suboblong; embryo three-quarters length of seed; color of endosperm grayish reddish orange or brownish orange; endosperm reddish brown mottled and usually pitted; scutellum edge broad (ca. 0.2–0.3 mm.), bandlike, at full maturity almost black; radicle-plumule axis narrow, elevated, almost straight, and lighter in color than the scutellum edge; pericarp coarsely striate or reticulate.

Florets: Length (4.0)–6.0–(7.0) mm.; width 1.25 to 2.0 mm.; thickness ca. the same as the fruits; opaque or semiopaque; membranaceous; glabrous; color pale yellowish gray, light green or purplish tinged; florets 2 to 3 times as long as the fruits, completely enclosing them; lemma and palea tips subacute; nerves of the palea glabrous; the nerve of the lemma scabrous toward the tip; palea splits at fruit maturity.

Specimen illustrated: *H. W. Clark* 22; Nov. 22, 1904; east of depot grounds; Lake Maxinkuckee, Indiana.

Common name: Tall dropseed.

Geographic distribution: Vermont to Montana, south to Louisiana, Arizona and Texas; eastern Washington; prairies and sandy meadows.

Habit: Perennial.

Economic importance: Valuable for forage and erosion control; fairly palatable and a rapid grower; seldom planted intentionally but is usually present in the commercial mixed bluestem (*Andropogon* spp.) used for seeding purposes.

Occurrence in seed samples: Reported in bluestem (*Andropogon* spp.) and other native grasses and legumes, and in lespedeza (*Lespedeza* spp.) from Kentucky.

10. Sporobolus poiretii (Roem. and Schult.) Hitchc., Bartonia 14:32. 1932. Based on *Axonopus poiretii* Roem. and Schult. PLATE 2,D

Axonopus poiretii Roem. and Schult., Syst. Veg. 2:318. 1817. Based on *Agrostis compressa* Poir., "n. 78", not *A. compressa* Willd., 1790, nor Poir. (op. cit.) No. 82, on the following page.

Agrostis compressa Poir. in Lam., Encycl. Suppl. 1:258. 1810, not *A. compressa* Willd., 1790, nor Poir. (op. cit.) 1:259. 1810, nor *Sporobolus compressus* Kunth, 1933. Carolina, *Bosc.*

Fruits: Length (0.8)–1.1–(1.4) mm.; width (0.5)–0.6–(0.8) mm.; thickness (0.2)–0.3–(0.4) mm.; translucent or opaque; shape oblongish, tapering to the base; usually strongly laterally compressed, the edges often reddish black rimmed from the mucilaginous pericarp; color of the endosperm and radicle-plumule axis reddish or yellowish orange; embryo less than half the length of the seed; scutellum edge elevated, about 0.1 mm. wide, and reddish black at maturity; pericarp minutely striate, the striations often dark reddish; pericarp becoming mucilaginous at seed maturity, causing the fruits to adhere to the florets.

Florets: Length 1.5–2.0 mm.; width and thickness ca. the same as for the fruits; semiopaque; membranaceous; essentially glabrous, but microscopically sparingly scaberulous; color stramineous or pale plumbeous; lemma acute; palea obtuse, erose; palea splits at fruit maturity; fruits with the pericarp partially slipped off often sticking to the lemma and palea; florets often affected with a black fungus.

Specimen illustrated: *A. S. Hitchcock* 523; March 1903; Miami, Florida.

Common names: Smutgrass; rattail smutgrass.

Geographic distribution: Virginia to Tennessee and Oklahoma, south to Florida, Texas, and the warmer parts of America to Argentina; on ballast in Oregon and New Jersey; tropical Asia, apparently introduced in America; open ground and waste places.

Habit: Perennial.

Economic importance: None reported in the United States; utilized for forage in arid regions in southern Europe, according to Fiori (1923).

Occurrence in seed samples: Reported as occurring in Dallis grass (*Paspalum dilatatum*) and in bluestem (*Andropogon* spp.) seed samples.

11. Sporobolus airoides (Torr.) U. S. Rep. Expl. Miss. Pacif. 7: 21. 1856. Based on *Agrostis airoides* Torr. PLATE 2,E

Agrostis airoides Torr., Ann. Lyc. N. Y. 1: 151. 1824. Branches of the Arkansas River near the Rocky Mountains, *James.*

Fruits: Length (0.9)–1.1–(1.7) mm.; width (0.5)–0.7–(0.9) mm.; thickness (0.4)–0.5–(0.7) mm.; opaque; shape irregularly suboblong or suboval; plump; the stylar tip rounded and not much laterally compressed; color of endosperm and embryo area about the same: a dull, dark, yellowish brown or light brown; endosperm rarely reddish flecked; embryo frequently over half the length of the seed; pericarp strongly dark reddish or blackish striate or reticulate, rarely slipped off mature fruits.

Florets: Length (1.5)–1.9–(2.5) mm.; width and thickness ca. the same as for the fruits; opaque or semitransparent; membranaceous; essentially glabrous but at high magnifications minutely scaberulous; color plumbeous, stramineous or purplish, often bronze tinged; lemma and palea acute or subacute, the nerves scaberulous toward the tips; florets spread apart at maturity, exposing the tips of the fruits; palea splits at fruit maturity.

Specimen illustrated: *Edgar A. Mearns* 2303; Sept. 11, 1893; near White Water, on Mexican boundary line; New Mexico.

Common name: Alkali sacaton; bunchgrass.

Geographic distribution: South Dakota and Missouri to eastern Washington, south to Texas and southern California; Mexico; meadows and valleys, especially in moderately alkaline soil.

Habit: Perennial, in large, tough bunches.

Economic importance: Excellent results from seeding in alkaline lowlands; valuable forage and erosion control plant.

Occurrence in seed samples: Occasionally part of native grass or legume seed samples or received as pure seed samples.

12. Sporobolus wrightii Munro ex. Scribn., Bull. Torrey Bot. Club 9:103. 1882. Pantano, Arizona, *Pringle.* PLATE 2,F

Fruits: Length (0.9)–1.3–(1.7) mm.; width (0.4)–0.7–(0.9) mm.; thickness (0.3)–0.5–(0.7) mm.; opaque (occasionally semitranslucent); plump; shape predominantly ovoid, plumper toward the base (rarely suboval or obovoid); stylar tip usually pointed and strongly laterally compressed; color of endosperm and embryo area about the same: a dull, dark reddish brown or occasionally light brown; endosperm usually faintly reddish flecked; embryo frequently less than half the length of the seed; pericarp strongly dark reddish or blackish striate or reticulate, frequently slipped off mature fruits.

Florets: Essentially the same as for *S. airoides.*

Specimen illustrated: *Edgar A. Mearns* 2345; Sept. 16, 1893; Dog Spring, Dog Mountains, New Mexico.

Common name: Sacaton.

Geographic distribution: Southern and western Texas and Oklahoma to southern California and central Mexico; mesas and valleys.

Habit: Perennial, in large dense tufts.

Economic importance: Excellent results from seeding in southern New Mexico; useful for grazing when young; also furnishes hay and and makes good winter range.

Occurrence in seed samples: Occasionally part of native grass seed mixtures; received as pure seed samples in U. S. Department of Agriculture Soil Conservation Service seed laboratories.

13. Sporobolus buckleyi Vasey, Bull. Torrey Bot. Club 10:128. 1883. Texas, *Buckley.* PLATE 3,A

Fruits: Length (0.7)–0.8–(1.0) mm.; width (0.3)–0.5–(0.7) mm.; thickness (0.2)–0.3–(0.4) mm.; translucent or opaque; shape suboval or broadly ovoid; plump and flattish at the base, the embryo without a prominent overhang; laterally compressed at stylar tip; color of endosperm and embryo light orange reddish, the embryo sometimes slightly darker; endosperm faintly light reddish flecked and pitted; embryo area inconspicuous, usually less than half the length of the seed; hilum within a basally prominent, black half-rim; pericarp usually minutely reddish striate.

Florets: Length 1.2 to 1.7 mm. long; width and thickness ca. the same as for the fruits; opaque; membranaceous; essentially glabrous, but microscopically slightly scaberulous, especially on the nerves; color plumbeous, purplish or stramineous; lemma acute, longer than the palea, which is subacute or obtuse; palea splits at fruit maturity; fruits with the pericarp partially slipped off often sticking to the florets.

Specimen illustrated: *Jason R. Swallen* 1492; Apr. 10, 1931; deep shade, in Rabb Palm Grove; Brownsville, Texas.

Common name: Buckley dropseed.

Geographic distribution: Texas and eastern Mexico.

Habit: Perennial.

Economic importance: Not reported.

Occurrence in seed samples: Not reported.

14. Sporobolus pulvinatus Swallen, Journ. Washington Acad. Sci. 31:351. f. 4. 1941. Adamana, Arizona, *Griffiths* 5107. PLATE 3,B

Fruits: Length (0.8)–0.9–(1.0) mm.; (0.4)–0.6–(0.7) mm.; thickness (0.2)–0.4–(0.5) mm.; semitranslucent; shape obovoid; obtuse at stylar tip and pointed at the base from the overhanging embryo; ventral surface frequently longitudinally grooved; color of the endo-

sperm yellowish gray or yellowish orange; endosperm often microscopically pitted; embryo area conspicuous, greenish black at maturity; scutellum in dorsal view panduriform; in lateral view of the fruit the inner scutellum reflected in a broad, dark semicircle through the semitranslucent endosperm; radicle-plumule axis broad in relation to the scutellum edge; pericarp finely striate.

Florets: Length (1.4)–1.5–(1.7) mm.; width and thickness ca. the same as for the fruits; semiopaque or opaque; membranaceous; essentially glabrous, but microscopically sparingly scaberulous; color stramineous or plumbeous, sometimes purplish tinged; lemma acute or subobtuse; palea the same length or slightly shorter than the lemma, obtuse, slightly dentate; palea splits at fruit maturity; fruits with the pericarp partially slipped off often sticking to the florets.

Specimen illustrated: *A. S. Hitchcock* 7820; Oct. 15, 1910; along street; El Paso, Texas.

Common name: None given.

Geographic distribution: Texas, New Mexico and Arizona; northern Mexico; sandy land.

Habit: Annual.

Economic importance: Not reported.

Occurrence in seed samples: Not reported.

15. Sporobolus pyramidatus (Lam.) Hitchc., U. S. Dep. Agr. Misc. Pub. 243:84. 1936. Based on *Agrostis pyramidata* Lam. PLATE 3,C

Agrostis pyramidata Lam., Tabl. Encycl. 1:161. 1791. South America.

Fruits: Length (0.7)–0.8–(1.0) mm.; width (0.4)–0.5–(0.6) mm.; thickness (0.2)–0.3–(0.4) mm.; usually translucent; shape obovoid, suboval, or subelliptic; obtuse at stylar tip and pointed at the base from the overhanging embryo; ventral surface occasionally longitudinally grooved; color of the endosperm light orange reddish; endosperm often microscopically pitted; embryo area conspicuous, dark reddish brown at maturity; scutellum in dorsal view panduriform; in lateral view of the fruit the inner scutellum reflected in a broad, dark semicircle through the translucent endosperm; pericarp finely striate.

Florets: Length (1.2)–1.5–(1.9) mm.; width and thickness ca. the same as for the fruits; semiopaque or opaque; membranaceous; essentially glabrous, but microscopically sparingly scaberulous; color stramineous or plumbeous; lemma acute, usually slightly longer than the palea; palea subacute or obtuse; palea splits at fruit maturity; fruits with the pericarp partially slipped off often sticking to the florets.

Specimen illustrated: *A. S. Hitchcock* 5343; June 27, 1910; sand, along railway near bay; Corpus Christi, Texas.

Common name: Whorled dropseed.

Geographic distribution: Kansas and Colorado to Louisiana and

Texas; southern Florida; tropical America; sandy or gravelly soil, especially along streets and along the seashore and in the interior in alkaline soil.

Habit: Perennial, in spreading or prostrate tufts.

Economic importance: Too short to be a productive grass; reported by Parodi (1928) as good in saline soils of the pampas, Argentina, where other types of pasture grasses are scarce.

Occurrence in seed samples: Not reported.

16. Sporobolus flexuosus (Thurb.) Rydb., Bull. Torrey Bot. Club 32:601. 1905. Based on *Sporobolus cryptandrus* var. *flexuosus* Thurb.

PLATE 3,D

Sporobolus cryptandrus var. *flexuosus* Thurb. in S. Wats., Bot. Calif. 2:269 1880. Based on *Vilfa cryptandra* var. *flexuosa* Thurb.

Vilfa cryptandra var. *flexuosa* Thurb. ex. Vasey, in Rothr., in Wheeler U. S. Survey W. 100th Merid. Rept. 6: 282. 1878. Nevada and Arizona, *Wheeler Exped.*

Fruits: Length (0.7)–0.8–(0.9) mm.; width (0.5)–0.6–(0.8) mm.; thickness (0.2)–0.4–(0.5) mm.; opaque, semitranslucent or translucent; shape asymmetrically broadly ovoid; pointed at the base from the overhanging embryo; obtuse and scarcely laterally flattened at stylar tip; in ventral and dorsal views predominantly oblongish, frequently "pinched" laterally toward the center; color of endosperm light yellowish brown or pale orange yellow, sometimes almost white; endosperm usually microscopically pitted and internally strongly "starchy" or granularly mottled; embryo area conspicuous, rusty or light reddish brown; radicle-plumule axis narrow, elevated, almost straight; in lateral view the scutellum edges usually unevenly reflected through the endosperm; pericarp frequently purplish or rusty striate.

Florets: Length (1.5)–2.1–(2.7) mm.; otherwise like *S. cryptandrus.*

Specimen illustrated: *Starr* 171A; Oct. 4, 1935; New Mexico.

Common name: Mesa dropseed.

Geographic distribution: Western Texas to southern Utah, Nevada, southern California, and northern Mexico; mesas.

Habit: Perennial.

Economic importance: Fair palatability; invader; occurs in lower Sonoran Zone on medium or light textured soils; at the present time the only species available for seeding around Las Cruces, Deming, and Lardsburg, New Mexico, on light-textured soils.

Occurrence in seed samples: Occasional pure seed samples in U. S. Department of Agriculture Soil Conservation Service seed laboratories.

17. Sporobolus nealleyi Vasey, Bull. Torrey Bot. Club 15:49. 1888, name only; Contr. U. S. Nat. Herb. 1:57. 1890. Brazos Santiago, Tex., *Nealley.*

PLATE 3,E

Fruits: Length (0.7)–0.8–(1.0) mm.; width (0.3)–0.4–(0.5) mm.; thickness (0.2)–0.2–(0.3) mm.; opaque or semitranslucent; shape

narrowly ovoid or narrowly obtuse at stylar tip; pointed at the base from the overhanging embryo; color of endosperm light yellowish brown or pale orange yellow, frequently almost white; endosperm sometimes microscopically pitted and usually internally "starchy" or granularly mottled; embryo area conspicuous, rusty or purplish brown; radicle-plumule axis narrow, elevated, almost straight; in lateral view the scutellum edges usually unevenly reflected through the endosperm; pericarp very finely striate, frequently purplish striate, sometimes rusty striate.

Florets: Length (1.5)–1.7–(2.0) mm.; florets usually opaque and very dark green or purplish tinged; otherwise like *S. cryptandrus*.

Specimen illustrated: *J. D. Schoeller & R. S. Campbell* 462; Forest Service 49290; Nov. 13, 1925; three-quarters of a mile east of Middle Well, in Caliche, Jornada Range Reserve, New Mexico.

Common name: Nealley dropseed.

Geographic distribution: Western Texas, Nevada, New Mexico, and Arizona; gypsum sands.

Habit: Perennial, with rhizomes.

Economic importance: Quite common around Roswell, Carlsbad, and Partalu, New Mexico; thought to have forage value.

Occurrence in seed samples: Not reported.

18. Sporobolus contractus Hitchc., Amer. Journ. Bot. 2:303. 1915. Based on *Sporobolus strictus* Merr. PLATE 3,F

Sporobolus strictus Merr., U. S. Dep. Agr., Div. Agrost. Cir. 32:6. 1901, not *S. strictus* Franch., 1893. Based on *Sporobolus cryptandrus* var. *strictus* Scribn.

Sporobolus cryptandrus var. *strictus* Scribn., Bull. Torrey Bot. Club 9:103. 1882. Camp Lowell, Arizona, *Pringle*.

Fruits: Length (0.8)–1.0–(1.2) mm.; width (0.4)–0.6–(0.8) mm.; thickness (0.2)–0.3–(0.5) mm.; opaque, semitranslucent or translucent; shape broadly ovoid or broadly elliptic; pointed at the base from the overhanging embryo; strongly laterally flattened; obtuse or pointed at stylar tip; color of endosperm light yellowish brown or pale orange yellow, sometimes almost white; endosperm usually microscopically pitted and internally strongly "starchy" or granularly mottled; embryo area conspicuous, rusty or light reddish brown; embryo area usually less than half the length of seed; radicle-plumule axis narrow, elevated, almost straight; in lateral view the scutellum edges usually unevenly reflected through the endosperm; pericarp frequently rusty striate, sometimes greenish striate.

Florets: Length (1.5)–2.4–(2.9) mm.; specimens with stramineous or pale plumbeous florets exceeding those with darker florets; otherwise like *S. cryptandrus*.

Specimen illustrated: *O. B. Metcalfe* 780; Sept. 22, 1903; Gila River bottom near cliff; Grant County, New Mexico.

Common name: Spike dropseed.

Geographic distribution: Arkansas, Colorado to Nevada, south to western Texas, southeastern California, and Sonora; adventive in Maine; mesas, dry bluffs, and sandy fields.

Habit: Perennial.

Economic importance: Not used much in reseeding; fits in where *S. cryptandrus* and *S. flexuosus* overlap.

Occurrence in seed samples: Occasionally in native grass seed mixtures or in U. S. Department of Agriculture Soil Conservation Service seed laboratories, received as pure seed samples.

19. Sporobolus giganteus Nash, Bull. Torrey Bot. Club 25:88. 1898. Dona Ana County, N. Mex., *Wooton* 394. PLATE 4,A

Fruits: Length (1.0)–1.3–(1.9) mm.; width (0.6)–0.8–(0.9) mm.; thickness (0.3)–0.4–(0.5) mm.; otherwise essentially the same as for *S. contractus*.

Florets: Length (2.2)–2.9–(3.5) mm.; otherwise essentially the same as for *S. contractus*.

Specimen illustrated: *Paul C. Standley;* Oct. 13, 1906; sand hills, southwest of Mesilla, New Mexico.

Common name: Giant dropseed.

Geographic distribution: Oklahoma and western Texas to Colorado and Arizona; mesas and sandhills.

Habit: Perennial.

Economic importance: Minor forage and erosion control value; used on sand dunes in New Mexico with fair results; palatable plant on dunes and blow-out areas in Oklahoma.

Occurrence in seed samples: Occasionally in native grass seed mixtures or in U. S. Department of Agriculture Soil Conservation Service seed laboratories as pure seed samples.

20. Sporobolus cryptandrus (Torr.) A. Gray, Man. 576. 1848. Based on *Vilfa cryptandra* Torr. PLATE 4,B

Vilfa cryptandra Torr. ex. Trin., Mém. Acad. St. Pétersb. VI. Sci. Nat. 4[1]:69. 1840. Based on *Agrostis cryptandra* Torr.

Agrostis cryptandra Torr., Ann. Lyc. N. Y. 1: 151. 1824. Canadian River (Texas or Oklahoma), *James*.

Fruits: Length (0.6)–0.8–(1.3) mm.; width (0.3)–0.5–(0.8) mm.; thickness (0.2)–0.3–(0.5) mm.; translucent, semitranslucent, or opaque; shape ovoid or obovoid (rarely suboval); pointed at the base from the overhanging embryo; laterally compressed toward the stylar tip; bulging toward the base; in ventral and dorsal views predominantly lance-shaped; color of endosperm moderate orange, brownish orange or light reddish brown; endosperm faintly light reddish or rusty flecked and usually pitted; endosperm internally clear or "starchy" or granularly mottled; embryo area usually inconspicuous, the same

color or a slighly deeper shade than the endosperm (rarely very much darker); radicle-plumule axis narrow, elevated, almost straight; in lateral view the scutellum edges evenly or unevenly reflected through the endosperm; pericarp very finely striate, sometimes faintly rusty or reddish striate (rarely with purplish striations).

Florets: Length (1.4)–1.8–(2.0) mm.; width and thickness ca. the same as for the fruits; opaque, transparent or semitransparent; membranaceous; glabrous to minutely microscopically scaberulous, especially toward the tips of the florets and the nerves; color variable, from plumbeous, frequently purple tinged, to stramineous; lemma and palea acute or acuminate; palea splits at fruit maturity.

Specimen illustrated: *Eula Whitehouse* 17190; Sept. 25, 1946; sandy prairie; 4 miles southeast of Farwell on highway 84; Parmer County, Texas.

Common name: Sand dropseed.

Geographic distribution: Maine and Ontario to Alberta and Washington, south to North Carolina, Indiana, Louisiana, southern California, and northern Mexico; sandy, open ground.

Habit: Perennial, usually in rather small tufts.

Economic importance: An invading species in many types of soils; more valuable for erosion control and seeding on problem spots than for forage; not as palatable as most other range grasses.

Occurrence in seed samples: Reported in native grass and legume seed samples or received as pure seed samples.

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THE WOODS AND FLORA OF THE FLORIDA KEYS: CAPPARACEAE

By WILLIAM L. STERN, GEORGE K. BRIZICKY,
AND FRANCISCO N. TAMOLANG

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THE WOODS AND FLORA OF THE FLORIDA KEYS: CAPPARACEAE

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Introduction

Capparaceae [3] A. L. de Jussieu, are primarily a tropical and subtropical family of xerophilous and heliophilous trees, shrubs, vines, and herbs characterized by acrid juice. The family comprises about 45 genera with approximately 700 species which are widely distributed in the New and Old Worlds. Almost half the genera are monotypic. Representatives of two pantropical genera occur on the Florida Keys: the native *Capparis* L., and *Cleome* L., which is probably naturalized. The present study deals only with the woody *Capparis*. (An excellent discussion of the taxonomic status of Capparaceae, ecology, morphology, pollination mechanisms, and distribution, is given in Jacobs, 1960.)

Capparis is a pantropical genus of about 250 species, best represented in America and Africa. Pax and Hoffmann (1936) subdivided *Capparis* into 14 sections. These appear to be fairly natural, although they are based almost exclusively on exomorphic, and perhaps not always unquestionable, characters. Chromosome numbers are known for a few species (2n=18, 30, 38, 40, 84; Darlington and Wylie, 1956) and can hardly be of any assistance at the present time. The genus as a whole appears to be insufficiently known; more comprehensive investigations based on adequate material, and a revision would be desirable. The two species of *Capparis* which occur on the Florida Keys probably represent two sections of the genus, as noted below.

Capparaceae, usually placed in the order Rhoeadales near Papaveraceae and Fumariaceae, are presently assumed to be most closely

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[1] Previous numbers in this series appeared in the journal *Tropical Woods* (Yale University, School of Forestry) under the running title, "The Woods and Flora of the Florida Keys": "Introduction" by W. L. Stern and G. K. Brizicky, vol. 107, pp. 36–65, 1957; "Compositae" by S. Carlquist, vol. 109, pp. 1–37, 1958; "Goodeniaceae" by W. L. Stern and G. K. Brizicky, vol. 109, pp. 38–44, 1958; "Passifloraceae" by W. L. Stern and G. K. Brizicky, vol. 109, pp. 45–53, 1958; and "Wood Anatomy and Phylogeny of Batidaceae" by J. McLaughlin, vol. 110, pp. 1–15, 1959.

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[3] This taxon is more widely known as Capparidaceae. However, the authors have chosen to follow the recommendations in Appendix II, "Nomina familiarum conservanda," of the 1961 edition of the *International code of botanical nomenclature*, where the approved name is Capparaceae.

related to Cruciferae, with affinities to Moringaceae, Resedaceae, and Tovariaceae. Hutchinson's (1926) order Capparales ("Capparidales") has been considered by Takhtajan (1959) to comprise all the above-mentioned families and Koeberliniaceae. Papaveraceae and Fumariaceae are excluded. Data from the biochemistry of these families (Hegnauer, 1961) seem to be in favor of the Takhtajan delimitation of Capparales. However, conclusions based on these data should probably be considered preliminary, since the material investigated is inadequate.

This study is based in large part on the wood specimens listed in table 1; these are on deposit for reference in several institutions including the division of plant anatomy of the U.S. National Museum. Associated herbarium vouchers from the U.S. National Herbarium, and other institutions, have also been examined where necessary. Microscope slides of wood prepared expressly for this research are on deposit in the division of plant anatomy.

Capparis cynophallophora L. Sp. Pl. 504. 1753.
Capparis jamaicensis Jacq. Enum. Pl. Carib. 23. 1760.

The Jamaica caper, *Capparis cynophallophora*, is a shrub or small tree with lepidote branchlets. Leaves are elliptical, oblong-elliptical or narrowly elliptical, rounded or notched at apex, rounded at base, not conspicuously reticulate-veined, glabrous on the upper surface, rusty or silvery lepidote with peltate trichomes on the lower surface, and exstipulate. Flower buds are 4-angled. The opened flowers are about 3 cm. in diameter. Sepals are more or less equal (appearing 1-seriate), free, lanceolate to ovate-lanceolate, acute, and valvate in aestivation. The receptacular nectariferous glands are liguliform. Staminal filaments are purplish. The one-locular ovary develops a torulose fruit-body which is lepidote, and 20–30 cm. long. The seeds are more or less reniform, and the embryo is coiled (cochleate).

DISTRIBUTION.—*C. cynophallophora* occurs in exposed areas in the coastal hammocks on most of the Florida Keys. It can be found in similar habitats north to Pine Key, Boca Ciega Bay (Pinellas Co.) and Cape Canaveral (Brevard Co.) on peninsular Florida. The Jamaica caper probably occurs on all the West Indian Islands, southern Mexico, Central America, and northern South America. In Panama, specimens from both coasts have been seen.

Capparis flexuosa (L.) L. Sp. Pl. Ed. 2. 722. 1762.
Capparis cynophallophora L. Syst. Nat. Ed. 10. 2:1071. 1759.
Morisonia flexuosa L. Pl. Jamaic. Pug. 14. 1759; Amoen. Acad. 5:398. 1760.

The limber caper, *Capparis flexuosa*, is a glabrous shrub or small tree with leaves of similar shape to *C. cynophallophora* (fig. 1). However, in this species, they are conspicuously reticulate-veined and

glabrous, minutely stipulate, and each bears an oblong, axillary gland. Subglobular flower buds open into blooms about 5–7 cm. in diameter. The sepals are unequal (distinctly 2-seriate), the exterior ones smaller than the interior, somewhat connate at the base, subcircular, and distinctly imbricate in aestivation. Receptacular nectariferous glands are broad and low appearing as glandular spots or pits. The staminal filaments are white. The ovary is 2-locular in the material investigated by W. R. Ernst.[4] Fruit-body (fig. 1) is continuous or somewhat torulose, glabrous, 10–20 cm. long; seeds are irregularly shaped, obliquely ellipsoidal, ovoid or obovoid, and slightly angular; the embryo is straight, and the cotyledons infold one another and cover the radicle with the lobes of their obliquely cordate bases.

DISTRIBUTION.—The range and habitat of *C. flexuosa* resemble those of the preceding, but this species appears to be more widespread. Specimens have been seen from as far north as Merritt Island (Brevard Co.) in Florida, from Mexican states on both coasts (north to Sinaloa on the west, and Tamaulipas on the east), from the West Indies, and from both coasts of Central America. The limber caper has been collected in Colombia, Ecuador, Venezuela, Paraguay, Trinidad and Tobago, and Brazil (Santa Catarina) in South America. Macbride (1938) thinks it probable that this species also occurs in Peru.

The nomenclatural confusion in which *Capparis cynophallophora* L. was usually known as *C. jamaicensis* Jacq., and *C. flexuosa* L. was known as *C. cynophallophora* L., was cleared up by Fawcett (1914). Although *C. cynophallophora* L. was placed into the section *Cynophalla* by Pax and Hoffmann (1936), the morphological characters[5] of this species clearly show that it belongs to the section *Quadrella* where De Candolle (1824) had already placed it. Radlkofer (1884, 1887) confirmed the place of *C. cynophallophora* ("*C. jamaicensis*") in this section, the original description of which he emended by adding some anatomical characters of the leaves.

Xylem Anatomy

The transverse section of *Capparis cynophallophora* L. exhibits alternating concentric bands of cells which make up the groundmass of the wood. Cells in these bands are nonseptate fiber-tracheids. Bands with cells having conspicuously wider lumina and somewhat thinner walls alternate with bands comprising narrow-lumened fiber-tracheids with thicker walls. These bands vary considerably in width, and adjacent bands commonly merge to form irregular arcuate

[4] Dr. Ernst has examined the Florida Keys capers in preparation for publishing "The genera of Capparaceae and Moringaceae in the southeastern United States" (1963).

[5] Four-angled flower buds, lepidote pubescence, equal and valvate sepals, and the presence of sclerenchymatous idioblasts ("*spicularis*") in the mesophyll of leaves.

segments. That these are bands associated with growth is evident from their formation and arrangement, but whether they are reflective of climatic conditions is questionable.

Fiber-tracheids have obscurely bordered pits which average 1.6 μ in diameter. The thickness of radial cell walls varies from thin to thick, and ranges from 0.62–4.20 μ with an average of 2.07 μ. The range in length of fiber-tracheids is from 292–661 μ with an average of 487 μ. Most cells fall between 415 and 523 μ in length.

The wood is diffuse-porous and pores are moderately small ranging from 8–107 μ in tangential diameter, averaging 62 μ wide. Most are between 33 and 83 μ in diameter. In transverse outline pores are circular to oval. There are normally 20 pores per square millimeter of which 24 percent are solitary. Mostly, however, pores are clustered and in radial multiples of 2–4 (5). Aggregations of pores present a complex picture appearing usually as somewhat irregular clusters of cells with one or two large central pores surrounded by several smaller, more or less wide-lumened cells. These aggregations, which shall be designated "pore complexes," consist of several cell types and modifications: "normal" vessels with regular elements, extremely narrow vessels, and axial parenchyma cells. Vessel element walls vary from thin to thick, from 1.7–5.0 μ, and average 3.8 μ. Mostly they range between 3.3 and 8.3 μ in thickness. Perforation plates are simple in even the very narrowest vessel elements, and are circular as viewed in the radial section. End walls of vessel elements (fig. 6) are mostly oblique and range from 0°–55° from the horizontal. Intervascular pitting is alternate, and the pits are crowded which sometimes produces angular pit borders. Pits are tiny, ranging from 2–3 μ in diameter, and appear to be obscurely vestured (cf. Bailey, 1933). However, this could not be determined with assurance on the sections available. Vessel elements average 192 μ in length and range from 94–296 μ. Most vessel elements are between 139 and 235 μ in length. Vessel–axial parenchyma pitting resembles the intervascular pitting in that it is alternate, but pits may be oblong in shape as well as circular.

Vascular rays (figs. 6, 7) as viewed on the tangential section are numerous and average 12 per mm. Most rays are uniseriate, but it is also common to see essentially uniseriate rays with short, bi- and triseriate central segments. Other rays are mostly bi- and triseriate throughout. Uniseriate rays are low and average 20 cells high (0.34 mm.). They vary from 4–30 cells (0.29–0.46 mm.) in height. The multiseriate rays are correspondingly low being roughly of the same dimensions as the uniseriate rays. Rays are essentially homocellular; that is, composed completely of procumbent cells (Kribs' homogeneous type I). Pitting between vascular ray cells and cells

of the axial parenchyma is alternate. Crystals occur more or less commonly in ray cells and fall within Chattaway's (1955) category 6, "rhomboidal, square or diamond-shaped."

Axial parenchyma is vasicentric consisting of a uniseriate sheath around pores or pore complexes, and sometimes it is also mixed among the cells in the complex. Crystals were not noted in axial parenchyma cells.

In *Capparis flexuosa* (L.) L., the banded nature of the imperforate tracheary elements of the groundmass (figs. 2, 3) as seen on the transverse section is not as sharply defined here as in the *C. cynophallophora* specimen described in the foregoing. The areas of narrow and wide-lumened cells are highly irregular, and the distinction between the areas is not sharp.

Imperforate tracheary elements of the groundmass are nonseptate fiber-tracheids characterized by small, minutely bordered pits (average 1.8 μ in diameter). Radial thickness of cell walls varies from very thin to thick, and ranges from 0.62–6.14 μ with an average of 2.25 μ. Fiber-tracheids range from 292–584 μ in length, averaging 418 μ. The most frequent range is between 385 and 492 μ.

The wood is diffuse-porous, the pores are circular to oval, and are moderately small varying from 21–96 μ with an average of 56 μ in tangential diameter (figs. 2, 3). Most are between 24 and 90 μ in width. There are about 35 pores per square millimeter of which 6 percent are solitary and the remainder in radial groups of 2–10 (mostly 2–5) with many irregular clusters. Pore complexes (figs. 2, 3) consist of a few large pores surrounded by other cells as noted above under the description of *C. cynophallophora*. Walls of vessel elements range from thin to thick, from 1.5–7.5 μ, and average 5.1 μ. Perforation plates are simple in all vessel elements and circular to oval. Vessel elements have oblique end walls which vary from 0°–70° from the horizontal. Intervascular pitting is alternate and crowded; the pits seem to be vestured and are very small (2–4 μ, average 3.2 μ) with circular to somewhat angular borders. Vessel elements range in length from 63–261 μ and average 175 μ. The most frequent range is between 156 and 210 μ. Vessel–axial parenchyma pitting is alternate and pits usually have circular borders.

Vascular rays as seen on the tangential section are numerous and average 10 per mm. Most rays are bi- and triseriate, uniseriate rays being of less frequent occurrence. Both uniseriate and multiseriate rays are low, the former ranging from 3–26 cells high (0.06–0.26 mm.), the latter ranging from 5–60 cells high (0.09–1.1 mm.). Rays are homocellular composed essentially of procumbent cells (Kribs' homogeneous type I). Multiseriate rays commonly have several-celled uniseriate wings. Pitting between ray and axial parenchyma

cells is alternate. Ray cells often contain crystals designated by Chattaway (1955) as "rhomboidal, square or diamond-shaped."

Axial parenchyma (figs. 2, 3) consists of a vasicentric sheath surrounding pores or pore groups. Strands may also occur among the vessels in the group. No crystals were seen in the cells of axial parenchyma.

Anatomical distinctions between the two species of *Capparis* collected from the Florida Keys, as described here, are slight. Minor variations in cell size occur, especially in the extreme ranges, but these are of little or no consequence considering the great coincidence of average figures and those for most frequent range. Most noticeable of the differences between the two species is the width of vascular rays. In *C. cynophallophora,* rays are largely uniseriate (figs. 6, 7), whereas in *C. flexuosa* bi- and triseriate rays predominate. Regardless, rays with bi- and triseriate segments occur in the former, and uniseriate rays appear in the latter. We may expect that this distinction then, is one of degree rather than the two conditions being mutually exclusive. A statistical analysis of many specimens of each species would doubtlessly determine the taxonomic validity of this potential anatomical distinction.

Analyses of Cells and Tissues

The descriptions above would seem to belie the complex nature of the wood, and especially the difficulties in interpretation of certain of the cellular components. In order best to interpret and evaluate the constituent elements of the wood in the Florida Keys capers, and for purposes of comparison, prepared slides of all species of *Capparis* were borrowed from the Samuel James Record Memorial Collection at Yale University; wood specimens of *Capparis* from the National Collections of wood were examined; and fluid-preserved specimens of the Keys species of *Capparis* were specially gathered for this study. All wood samples employed in these studies were associated with corresponding herbarium vouchers except as noted in table 1.[6] Furthermore, wherever possible vouchers were examined to substantiate the authenticity of identification; in some doubtful cases twigs from vouchers were examined microscopically and compared with the wood samples to assure concurrence.

[6] The authors are deeply indebted to Dr. Graeme Berlyn and Mr. Richard A. Mark of Yale University for the privilege of examining *Capparis* slides and some herbarium vouchers from the Record Memorial Collection, and to Mr. John R. Millar of the Chicago Natural History Museum for allowing us to see and compare herbarium vouchers of *Capparis* with wood specimens used for comparative studies. Dr. James A. Duke of the Missouri Botanical Garden aided in verifying the identification of some herbarium vouchers on deposit in St. Louis and for sending us bits of twigs for comparison. For his help in preparing slides, and for other kindnesses, the authors are grateful to Mr. Edward S. Ayensu, research assistant at the Smithsonian Institution. Particular gratitude is due Mr. George Stevenson of Plantation Key, Florida, and Dr. P. B. Tomlinson of the Fairchild Tropical Garden in Miami, Florida, for their most kind assistance in collecting fluid-preserved stems of *C. flexuosa* and *C. cynophallophora* together with herbarium vouchers.

GROUNDMASS.—After a preliminary study of the material on hand, we found that a convincing interpretation of the cells and tissues of the wood of *Capparis* would require fluid-preserved specimens. But nowhere was this need more strongly felt than in the correct identification of the cells comprising the tissues surrounding the pore complexes to be described below. Bands are more or less obvious on the transverse section of all woods examined (figs. 2, 3), except for *C. nitida* (fig. 4) and *C. schunkei*. At first it seems obvious that these bands are merely rings of growth demarcated by alternating layers of thick- and thin-walled imperforate tracheary elements. But, in *C. pulcherrima* and *C. angulata* (figs. 10, 11), it seems equally apparent that at least some of the bands are truly and purely parenchymatous. In certain species, e.g., *C. decidua*, a confounding of bands occurs; some seem to be totally prosenchymatous and others at least partly parenchymatous. One is tempted here to call this arrangement boundary parenchyma after the definition of Jane (1956). In *C. nitida* (fig. 4) and a few other species pore complexes are much simplified and seem to consist of a solitary pore, a short radial multiple, or a small cluster surrounded by a several- to many-seriate sheath of vasicentric parenchyma. In the slides prepared from previously dried wood, certain groundmass cells which look like imperforate tracheary elements (fibers) take on some of the characteristics of parenchyma (compare fig. 2 with fig. 3), i.e., cytoplasmic remains are present within the lumina. This was indicated by the strong affinity for haematoxylin shown by the cell contents. Walls are thinner in these cells than in adjacent prosenchymatous elements, and the compound middle lamella seems thicker and possesses a great affinity for haematoxylin and little for safranin. The foregoing observations raised questions in the minds of the authors which seemed solvable only after the examination of fluid-preserved rather than dried tissues.

For purposes of cytological examination, the fluid-preserved collections of Stevenson (Newcomer's fixative) and Tomlinson (F. A. A.) were utilized. In all, five specimens were available: two of *C. flexuosa*, two of *C. cynophallophora*, and a single, unnamed specimen from the Fairchild Tropical Garden. Our observations indicate that in the specimens of *Capparis* investigated a well-formed fusiform nucleus is present in every imperforate tracheary element, from bark to the inner edge of the radial section (i.e., for a distance of 6–10 mm.), in all but the Stevenson collection of *C. cynophallophora* (fig. 13). Here, the innermost elements lack a nucleus. Furthermore, starch grains occlude the cell cavity completely, except for the narrowed tips, of practically all imperforate tracheary elements in the specimens of *C. flexuosa* (fig. 13). In *C. cynophallophora* starch occurs mostly in the thick-walled imperforate tracheary elements at the margins of "growth

rings," but not in every cell. As in *C. flexuosa*, starch grains totally occlude the cell cavity. In the unnamed Tomlinson specimen starch occurs in bands corresponding to the alternating layers of thick- and thin-walled imperforate tracheary elements—it is present only in the thick-walled cells.

We may assume from the above that the imperforate tracheary elements of the groundmass in the five *Capparis* specimens under analysis, partake of the nature of parenchymatous cells. It is probable that they continue to perform vital as well as mechanical functions long after formation by the vascular cambium. In this connection it is interesting to consider Carlquist's (1961) remarks, which point out the possibility of axial parenchyma cells arising from libriform wood fibers through the mechanism of "fiber dimorphism."

These findings contrast strongly with the widely held characterization of imperforate tracheary elements as being dead at ontogenetic maturity. The living nature of these cells is indicated by the presence of a presumably functioning protoplast which, among other activities, stores starch. The cell wall pitting in these elements, however, consists of tiny vestigially bordered or simple pit-pairs, whereas in vasicentric parenchyma cells in the same specimen the pit-pairs are as large as intervascular pits, simple, half-bordered, or even fully bordered.

Fahn and Leshem (1963), in a study of xylem anatomy of woody desert plants from Israel and other woody plants native to Switzerland, reported living fibers in 70 percent of 60 species in 24 plant families. Furthermore, they state that fibers over the entire sapwood contained living protoplasts. Included in their study was *Capparis spinosa* L. which showed living fibers in the xylem. Esau (1953) mentions that "In contrast to other wood fibers, the septate forms long retain their protoplasts and serve for storage of starch, oils . . . ." Cumbie (1960) also mentions the presence of nucleated fibers in certain transitional herbaceous–woody legumes, and Carlquist has remarked on the presence of these in Compositae in correspondence with the authors. Harrar (1946) examined the wood of over two thousand species of plants from the Yale collections and recorded the presence of starch in the septate fiber-tracheids of many hundreds of these. It is reasonable to assume that these starch-containing cells, especially in sapwood, are living, and Harrar also believes they may function in a manner similar to axial parenchyma.

It is likely that further cytological studies based on fluid-preserved material of the stem will force us to revise, or at least to broaden, our currently held notions as to the physiological condition of the imperforate tracheary element. Our observations here, and those of Fahn, indicate relatively long-lived protoplasts in imperforate trache-

ary elements; furthermore, it is not only the septate fiber-tracheids which retain their vital functions for more or less long periods after formation; the phenomenon may also occur in nonseptate elements. The universality of this phenomenon still remains to be tested.

Interesting physiological questions concern the ultimate fate of this stored starch. If it is dissolved and subsequently transported, must a still-living cell be postulated? How does the dissolved starch pass from the storage cells to where it is "needed" elsewhere in the plant? The tiny pits in libriform fibers and fiber-tracheids would certainly present a significant barrier to free passage. Even then, through what cells would the dissolved starch be conducted?

These observations on fluid-preserved wood, coupled with those on previously dried wood, helped us considerably to interpret with a degree of assurance, the nature of the groundmass cells in *Capparis*. By and large, the cells of the groundmass are imperforate tracheary elements, either libriform wood fibers or fiber-tracheids.

AXIAL PARENCHYMA.—The growth rings are not to any extent dependent for distinction upon the occurrence of boundary parenchyma, and are visible because of alternating layers of thick- and thin-walled fibers (figs. 2, 3). The situation in *C. decidua*, where axial parenchyma cells are involved in growth-ring margins, is of sporadic occurrence on the transverse section, and is dependent on the presence of closely adjacent, tangential rows of pore complexes next to the growth-ring margin. The seemingly apotracheal parenchyma cells are in reality vasicentric parenchyma cells mixed among the cells of the groundmass at the growth-ring boundary.

All species have narrow sheaths of vasicentric parenchyma surrounding the pore complexes (figs. 2–4, 10, 11). Cells adjacent to these narrow sheaths which appear parenchymatous, as in *C. nitida* (fig. 4), are merely thin-walled, wide-lumened, imperforate tracheary elements as described above. In two species, *C. pulcherrima* and *C. angulata* (figs. 10, 11), true banded axial parenchyma occurs, as well as the vasicentric, and sometimes aliform and confluent configurations. These bands are composed of several uniform cell layers which contrast strikingly with the parenchymatous-appearing, thin-walled, prosenchymatous cells that mark the boundaries of growth rings in other species.

PORE COMPLEXES.—All species of *Capparis* investigated were characterized by the presence of more or less complicated groupings of pores and associated cells as observed on the transverse section (figs. 2, 3, 10, 11). These pore complexes consist of a few large vessels, a variable number of small vessels, sometimes imperforate tracheary elements, and always associated axial parenchyma. As indicated previously the latter is always paratracheal, forming a complete

sheath around the pore complex, and sometimes strands are intermixed among other elements within the complex. Parenchyma cells are relatively thick-walled and lignified. The tiny vessel elements which occur in association with the large vessel elements are interesting in that they always possess simple perforations (figs. 2, 3, 11, 12). They may be narrower than adjacent imperforate tracheary elements; sometimes they are imperfect and contain only a single perforation; and occasionally perforations appear on the axial walls.

To interpret these complexes solely on the transverse section is impossible. It is hardly possible to distinguish tiny pores from transverse sections of associated imperforate tracheary elements (figs. 2, 3, 10, 11). Without doubt then, our analyses of pore groupings are in error—an error difficult to overcome, for if there is a single feature of the wood which might be said to characterize *Capparis*, it is the pore complex described above.

Vascular rays.—Vascular rays in *Capparis* are essentially homocellular and are composed of procumbent cells (figs. 5–9). However, in a number of species—*C. decidua, crotonantha, linearis, oxysepala, quina, schunkei, tenuisiliqua, verrucosa,* and *angulata*—rows of squarish marginal cells are of sporadic occurrence, and it is possible that this phenomenon occurs in all species of *Capparis* to a certain extent. In some of the species examined other peculiarities are present to a more limited extent. Thus, inflated ray cells which resemble secretory cells of some lauraceous woods occur in *C. ferruginea, nobilis, quina,* and *tenuisiliqua;* and sheath cells are of infrequent occurrence in the rays of *C. nobilis, schunkei, verrucosa,* and *angulata.* Seriation of rays varies from 1–7 cells wide. Height of uniseriate rays is from 1–22 cells, of the multiseriate rays, from 3–55 cells (figs. 6–9).

Other features.—Storied structure occurs in only one of the species studied, *C. angulata* (fig. 9). The cells which comprise bands of parenchyma, and the vessel elements, are in marked seriation as viewed on the tangential section. Cozzo (1944, 1946) and Cozzo and Cristiani (1950) record partial storying in *C. salicifolia* Gris. and *C. tweediana* Eichl. Rhomboidal crystals were observed in most of the species under investigation, and it is probable that all species of *Capparis* possess the genetic potential to form crystals under conducive environmental circumstances. Most commonly, crystals were found in the ray cells, but sometimes they were also observed in the cells of the axial parenchyma.

Phylogenetic Specialization in the Wood

The structure of the wood of *Capparis* is indicative of a high level of evolutionary specialization, as shown by the presence of simple perforation plates in vessels and alternate intervascular pitting (figs.

FIG. 1. *Capparis flexuosa* (L.) L., Crawl Key, Florida; upper portion of shrub showing mature fruits, × 1/4 (*W. L. Stern 1519*, US).

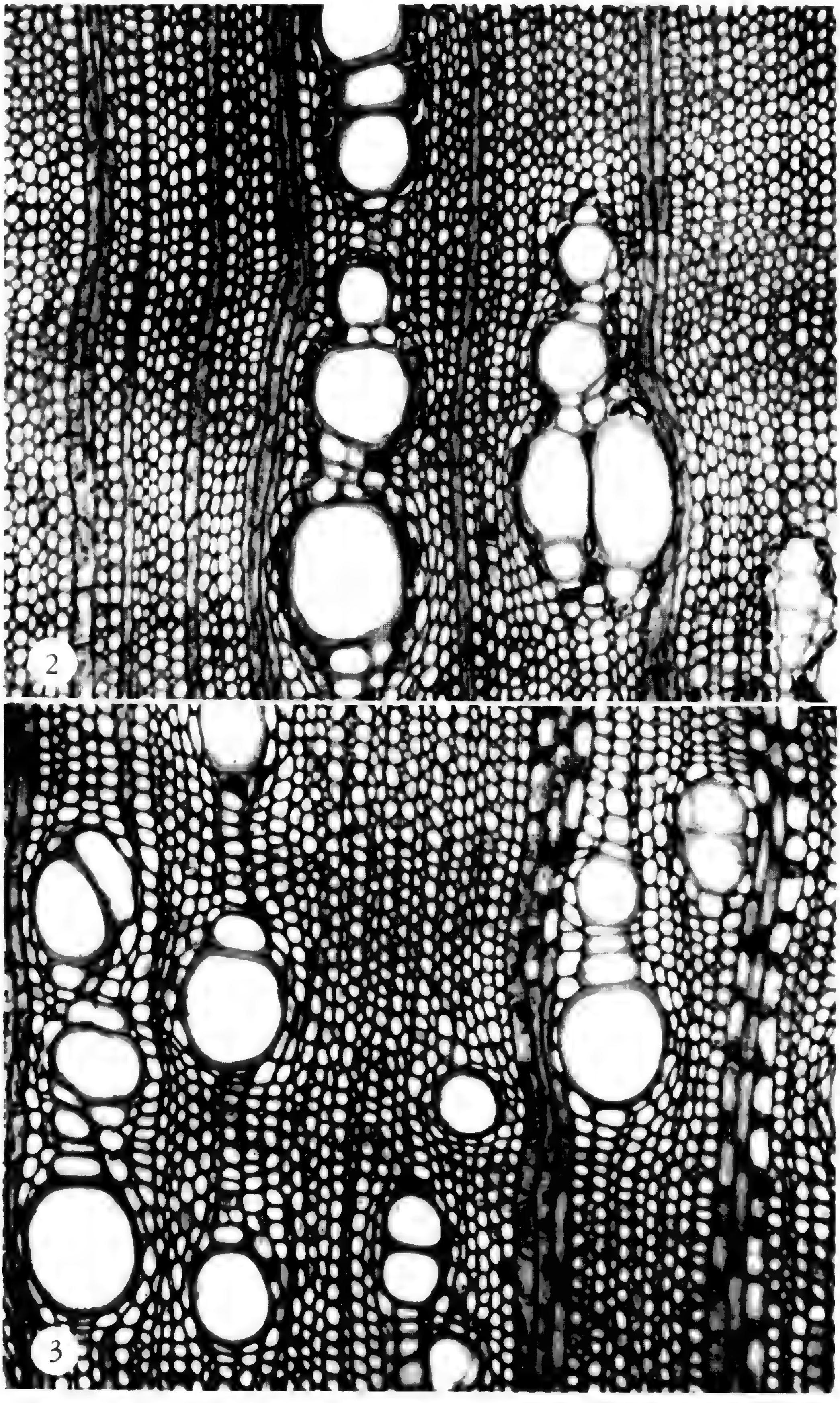

FIG. 2. *Capparis flexuosa* (L.) L., transverse section of wood illustrating pore complexes, and uniseriate sheath of vasicentric axial parenchyma which is discernible in this material prepared from fluid preserved tissues. × 160 (*G. Stevenson s.n.* USw 30300). FIG. 3. *C. flexuosa* (L.) L., transverse section for comparison with figure 2. Notice that on this section, prepared from dried tissues, it is not possible to distinguish the uniseriate sheath of axial parenchyma from the surrounding imperforate cells. × 160 (*J. G. Jack 5033*,

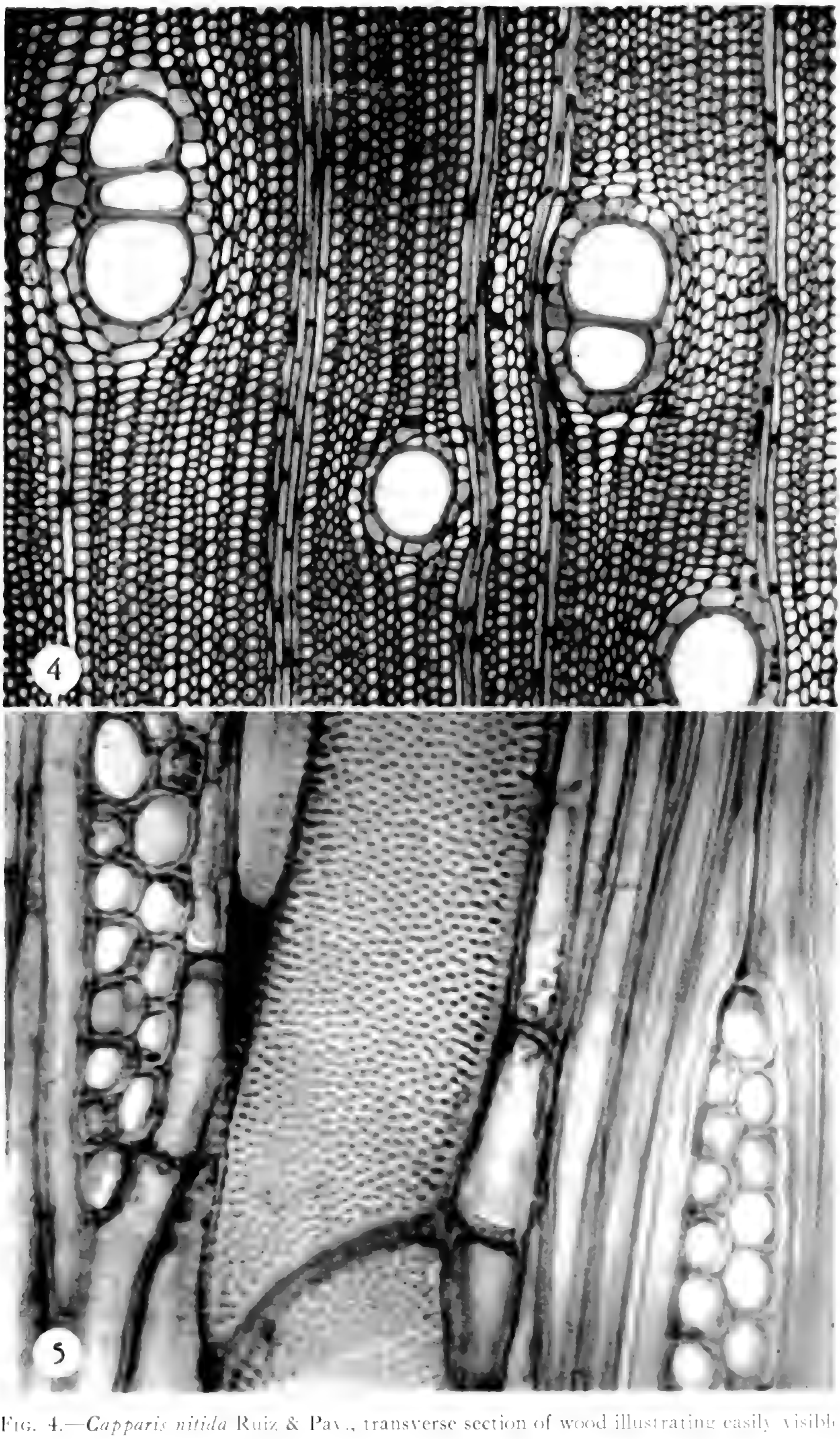

FIG. 4.—*Capparis nitida* Ruiz & Pav., transverse section of wood illustrating easily visible sheath of uniseriate vasicentric axial parenchyma, and uncomplicated arrangement of pores, × 160 (*Ll. Williams 5725*, Yw 18819). FIG. 5. *C[illegible]* [illegible] tangential section of wood showing alternate intervascular pitting, and homocellular vascular rays composed solely of procumbent cells, [illegible]45 (*Ll. Williams 6054*, Yw 19028)

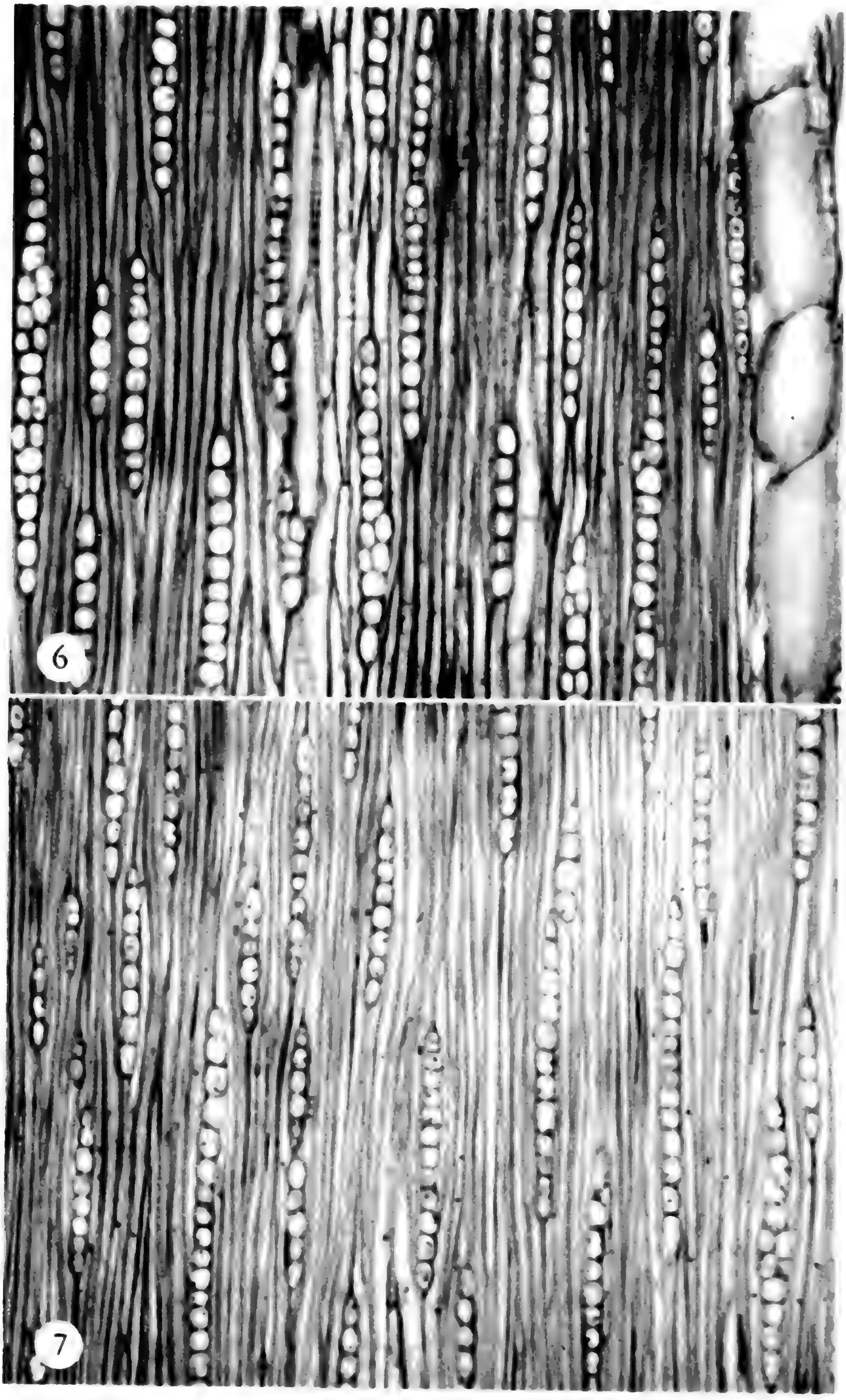

FIG. 6. *Capparis cynophallophora* L., tangential section of wood, × 200 (*G. Stevenson s.n.*, USw 30299). FIG. 7. *C. cynophallophora* L., tangential section of wood, × 200 (*P. B. Tomlinson 19.III.62A*). Vascular rays in these sections are illustrative of Group I type: mostly uniseriate with occasional biseriates bearing uniseriate extensions

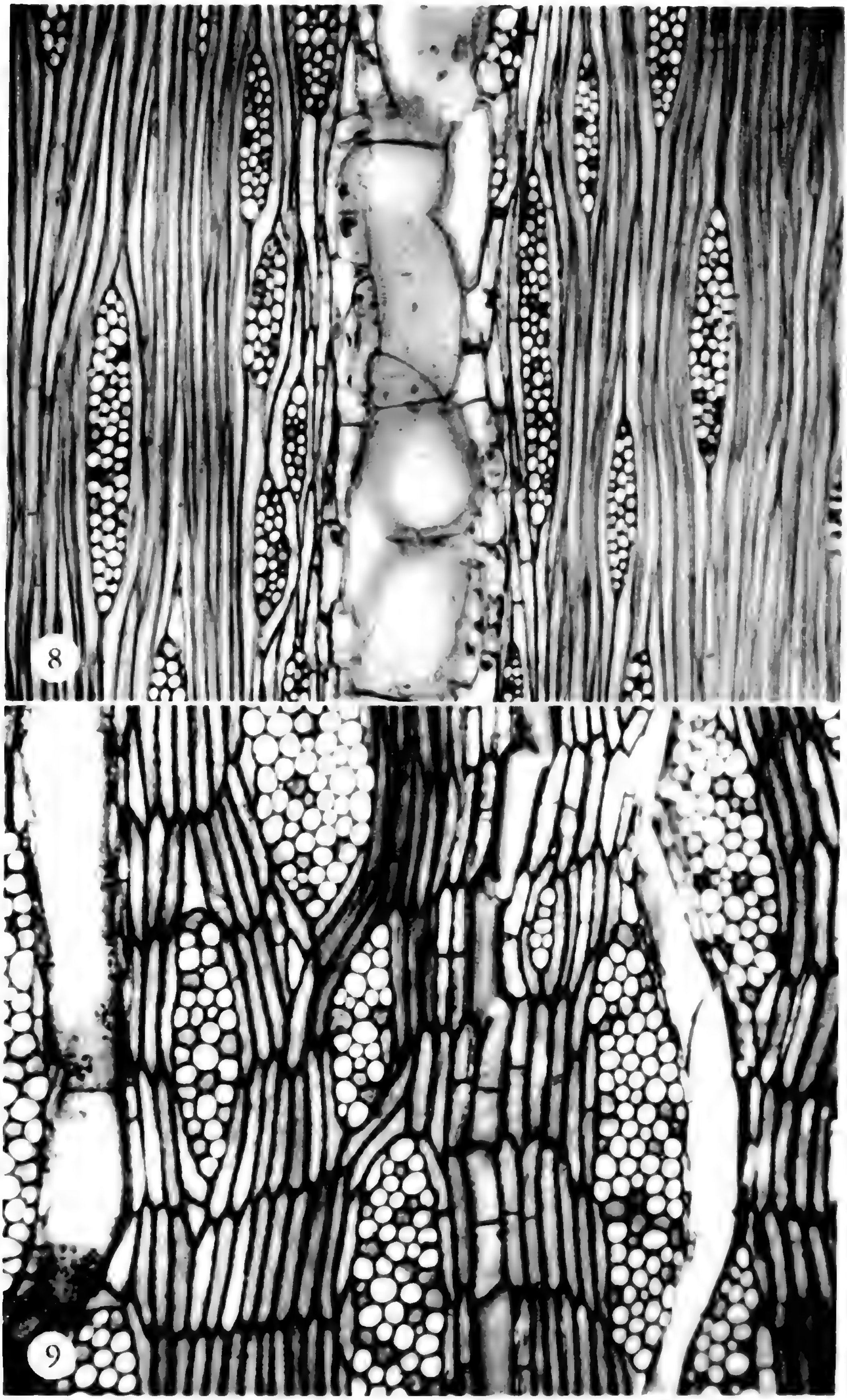

FIG. 8. *Calycophyllum spruceanum* Benth. ex Hook. f., tangential section of wood showing Crystal Heterocellular rays: multiseriate and fusiform. 160 (*L. Williams* 5725, USw 16016). FIG. 9. *Capirona decorticans* Spruce, tangential section of wood showing Crystal Heterocellular fusiform axial parenchyma cells, and multiseriate rays. 160 (*L. Williams* 5672, USw 16017).

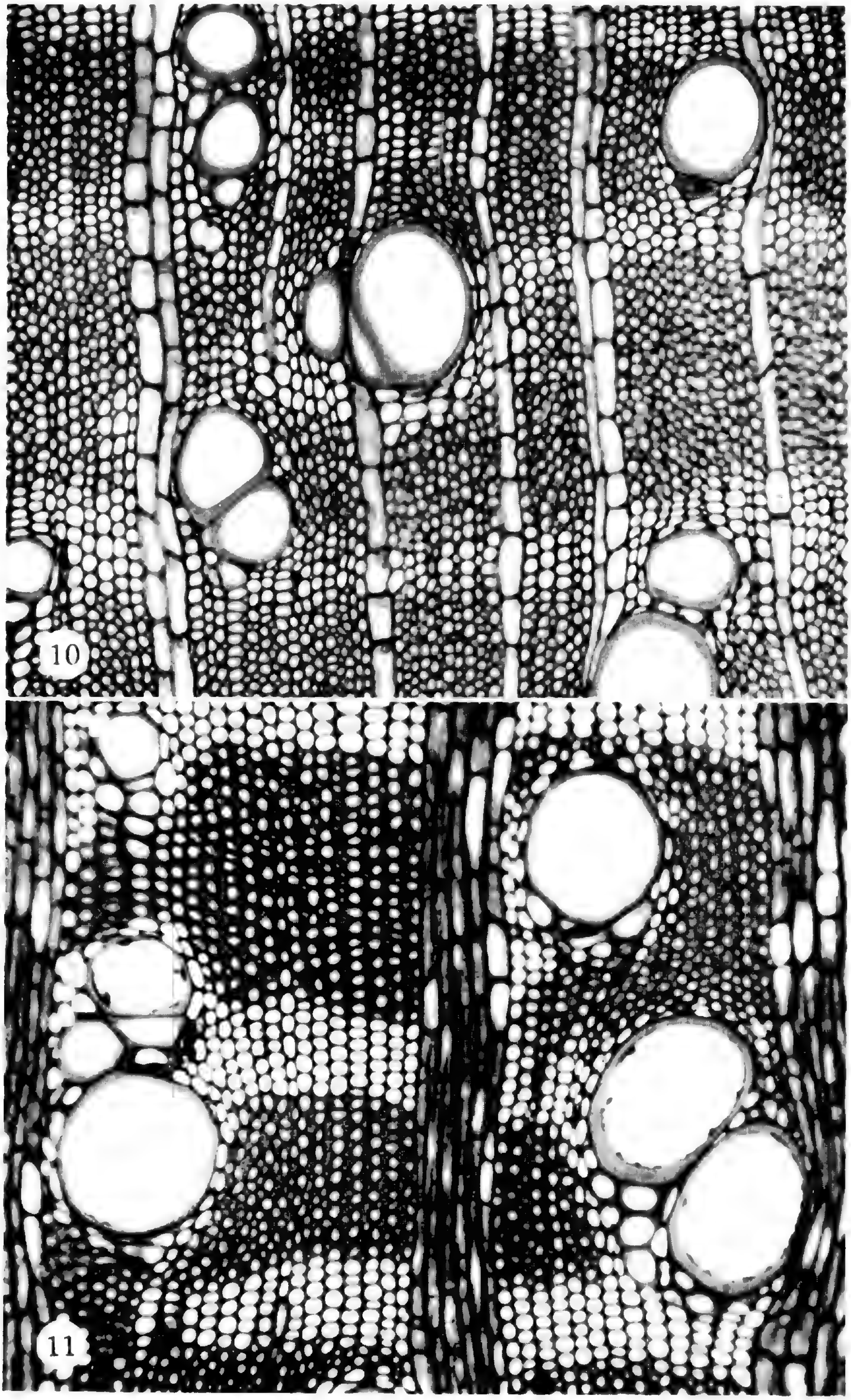

FIG. 10. *Capparis pulcherrima* Jacq., transverse section of stem showing lignified vessels and parenchyma. 160 (*A. Dugand 195, 159, Yw 23936*). FIG. 11. *C. amplectans* Ruiz & Pav., transverse section of stem showing lignified vessels and parenchyma. 160 (*F. Woytkowski 9072, US x 1901*).

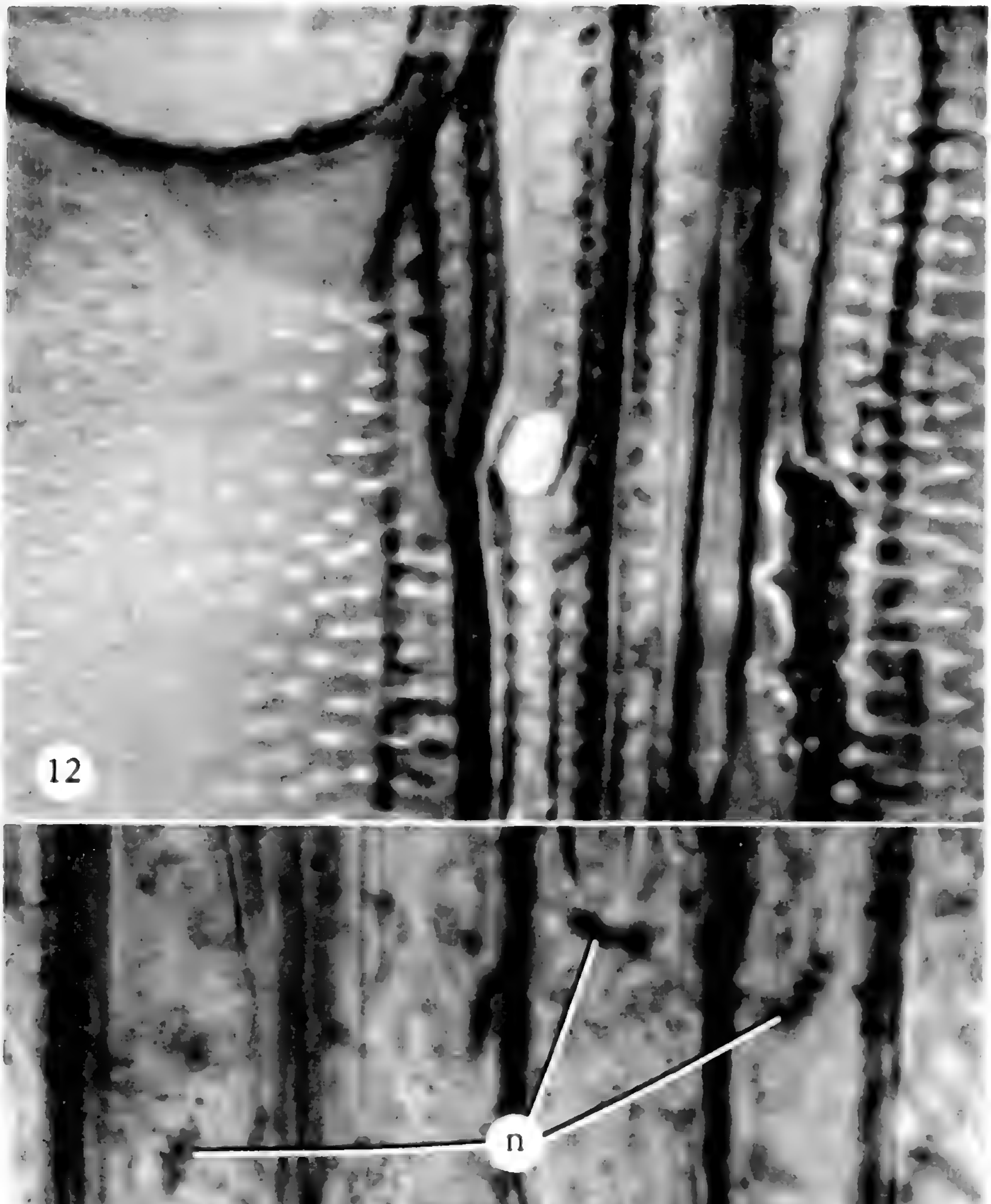

FIG. 12. *Capparis tenuisiliqua* Jacq., radial section of wood to show simple perforation of tiny vessel element (center) associated in complex with vessel of normal [illegible]. 1800 (*S. J. Record 80* Yw 16479). FIG. 13. *C. flexuosa* (L.) L., radial section of wood to demonstrate presence of fusiform nuclei, *n*, in fiber tracheids at 1 cm. distance from vascular cambium; starch grains are also visible in the lumina of the fibers [illegible]. 1375 (*G. Stevenson s.n.*, U Sw 30300)

5, 9, 12), the highly peculiar pore complexes (figs. 2, 3, 10, 11), paratracheal parenchyma and other parenchyma modifications (figs. 2–4, 10, 11), homocellular vascular rays (figs. 5–9), and imperforate tracheary elements with simple or vestigially bordered pits. This fact causes us to wonder at the relatively low taxonomic placement of Capparaceae and the comparative primitiveness of the families with which it is ordinarily associated in some schemes of plant classification.

The authors appreciate that the phylogenetic position of a family containing 45 genera cannot be established through a brief study of one genus using a single criterion, i.e., xylem anatomy. It is suggested, however, that Capparaceae, with almost 50 percent monotypic genera, may be a highly derived taxon in which the evolutionary links among the genera have passed out of existence over the ages. What remains today are the end-products of evolution; the connecting stages, in the form of transitional taxa, are extinct.

Bessey (1914) derives the Rhoeadales (containing Capparaceae) directly from Ranales; Engler and Diels (1936) also place Rhoeadales in close association with Ranales; and in the Bentham and Hooker (1862) system, Capparaceae are placed in the Parietales next to Ranales. Wettstein (1935) treats Capparaceae in Rhoeadales and mentions that they are related to both Cruciferae and Papaveraceae. Furthermore, he states that Capparaceae contain the types from which the Cruciferae could have arisen. Pax and Hoffman (1936) say that without doubt Capparaceae belong in Rhoeadales and are most closely allied to Cruciferae.

In light of the above, it is rather interesting to examine the position of Capparaceae in Hutchinson's (1959) treatment. Here they occur quite high in the Lignosae as the type of Capparales. He derives this order from the Dilleniales via Bixales and Pittosporales. Hutchinson regards the similarity in flower and fruit structure between Cruciferae and Capparales as parallel evolution. Futhermore, in addition to Capparaceae, Hutchinson includes Moringaceae and Tovariaceae (*Tovaria* is included in Capparaceae by Bentham and Hooker) in Capparales. Takhtajan (1954), like Hutchinson, gives Capparales a more derived placement in his scheme. He shows the order emanating from Cistales, along with Cucurbitales, Salicales, and Tamaricales. However, Takhtajan (1959) retains Cruciferae in Capparales, whereas Hutchinson includes it in Cruciales, a separate order.

Capparis wood differs markedly from that in some families ordinarily associated with Capparaceae (i.e., Papaveraceae, Cruciferae, and Resedaceae), in having homocellular rays consisting solely of procumbent cells. The pore complexes described above for *Capparis* have not been recorded in the woods of the Papaveraceae, Cruciferae,

or Resedaceae which are anatomically specialized along other lines (cf. Metcalfe and Chalk, 1950). In certain respects, the wood of *Moringa* resembles *Capparis* in that rays are homocellular and storied axial parenchyma is present. Metcalfe and Chalk (1950) place some emphasis on the presence of myrosin cells in parietalean taxa as a significant indicator of relationship. All the taxa mentioned above possess myrosin cells except Papaveraceae (Hegnauer, 1961). It is noteworthy in this regard that Moringaceae, which Hutchinson considers in his taxonomically elevated Capparales, is placed by Bentham and Hooker in Sapindales. Without the benefit of detailed anatomical and associated studies in the other genera of Capparaceae, and comparative investigations into the anatomy of Papaveraceae, Cruciferae, Resedaceae, and Moringaceae, a brief survey such as this of the anatomy of families reputedly related to Capparaceae can only lead to wild speculation. It is sufficient to say that our study lends some anatomical support to Takhtajan's and Hutchinson's placement of Capparaceae in a separate order, more highly placed than the parietalean families with which it is usually associated.

Anatomically, the most highly advanced species among those investigated appears to be *C. angulata*. That this is so is indicated by the combination of pronounced storying among the cells of the axial parenchyma and vessels, coupled with the highly modified banded, vasicentric, aliform, and confluent parenchyma distribution (figs. 9, 11). *C. pulcherrima* is also more highly specialized than the other species; it lacks the storied structure of *C. angulata*, but exhibits the same kind of parenchyma specialization (fig. 10).

Intrageneric Alignment

The species of *Capparis* can be divided into two groups based upon the seriation of rays. At first it seemed desirable to make a separation into three groups: (1) species with uniseriate rays, (2) species with rays having short multiseriate segments supporting several- to many-celled uniseriate wings, and (3) species with multiseriate rays and only a single apical cell, i.e., fusiform as viewed in the tangential section. However, closer scrutiny caused us to alter our course and to unite the first two groups. We found that woods with predominantly uniseriate rays always had some rays which fell into the second group, and woods in the second group often had many uniseriate rays (figs. 6, 7), so that apparently no consistent separation between groups 1 and 2 could be made (cf. remarks on anatomical distinction between *C. flexuosa* and *C. cynophallophora*). Therefore, only two groupings, based on ray width, were devised: (I) species with predominantly uniseriate rays, or with rays composed of short bi- (or tri-) seriate segments having conspicuous several- to many-

celled, uniseriate extensions (figs. 6, 7), and (II) species with predominantly multiseriate rays which appear fusiform on the tangential section and possess only one or two cells at their apices (figs. 8, 9). Further studies involving more species might show transitions between these two groups, but on the basis of this investigation they appear sufficiently exclusive of each other.

The species studied in our investigation were dispersed into the sections of *Capparis* recognized in the treatment of Pax and Hoffmann (1936). The appropriate ray classification was placed next to each binomial and the results are outlined in table 2. Although representation of species in the various sections is in some cases meager, it is noteworthy, excepting section *Cynophalla*, that the sections are homogeneous with respect to the ray type shown. Whether this taxonomic-anatomic device would stand up if further species were introduced, remains to be shown. Or, as may be the case in *Cynophalla*, the anatomical evidence may indicate a lack of taxonomic homogeneity within the section. Substantiation for the latter was mentioned previously. Recent work of W. R. Ernst has shown that *C. cynophallophora* belongs in section *Quadrella*, rather than *Cynophalla*.

Summary

Although *Capparis flexuosa* and *C. cynophallophora* are easily separated, even by their gross foliar morphology, the anatomical distinctions are more subtle, and possibly less reliable. In *C. cynophallophora*, vascular rays are largely uniseriate, whereas in *C. flexuosa*, bi- and triseriate rays predominate.

Observations made on sections cut from fluid-preserved material, showed that the banding in the wood of the two capers from the Florida Keys, and in other species, is caused solely by alternating layers of thick- and thin-walled prosenchymatous cells. Axial parenchyma is strictly paratracheal and is not normally a part of these bands. The groundmass is purely prosenchymatous. Fiber-tracheids in *C. flexuosa* and *C. cynophallophora* may remain living for longer or shorter periods after formation by the vascular cambium and ontogenetic maturity takes place in these cells. This phenomenon is probably more widespread than heretofore realized.

The wood anatomy of *Capparis* can be characterized by the presence of pore complexes, alternate intervascular pitting and simple perforation plates, paratracheal parenchyma, homocellular vascular rays, and imperforate tracheary elements with simple or vestigially bordered pits. Also, certain species exhibit storied structure. These features are all associated with phylogenetic advancement and indicate that

Capparis, and possibly Capparaceae, occupies a more derived position than it is usually afforded.

Using the seriation of vascular rays, the species of *Capparis* can be separated into two groups. These groups follow the Pax and Hoffmann sectional delimitations of the genus except for the section *Cynophalla*, which appears anatomically heterogeneous. Floral studies of the two Keys species of *Capparis*, both placed in *Cynophalla* by Pax and Hoffmann, give taxonomic support to this suggestion. More intensive studies on a broader sampling of species will probably produce at least two more anatomical features useful in separating the species of *Capparis:* configuration of the axial parenchyma, and presence or absence of storying. Application of these features will serve to test the proposed separation of *Capparis* by ray seriation, and may enable us further to refine our anatomical system.

TABLE 1.—*Specimens of* Capparis *wood examined*

[Citation of specimens follows the recommendations of Stern and Chambers (1960). WOOD COLLECTIONS: (USw) Smithsonian Institution, (Yw) Yale University School of Forestry. HERBARIA: (MO) Missouri Botanical Garden, (NY) New York Botanical Garden, (US) Smithsonian Institution, (Y) Yale University School of Forestry, (A) Harvard University Arnold Arboretum, (GH) Harvard University Gray Herbarium, (F) Chicago Natural History Museum, (Ilanoth) National and University Institute of Agriculture, Lev Hasharon, Israel.]

Species and Authority	*Collector and No.*	*Country of Origin*	*Wood Collection Catalog No.*	*Location of Vouchers*
angulata Ruiz & Pav.	F. Woytkowski 5672	Peru	USw 16017	MO
baducca L.	B. A. Krukoff 4665	Brazil	USw 9145	NY, US
baducca L.	B. A. Krukoff 4889	Brazil	USw 9248	NY, US
cynophallophora L.	J. G. Jack 5715	Cuba	Yw 16674	Y, A
cynophallophora L.	J. G. Jack 5809	Cuba	Yw 16695	?
cynophallophora L.	J. G. Jack 6742	Cuba	Yw 16746	?
cynophallophora L.	W. L. Stern & G. K. Brizicky 262	U.S.A. (Fla. Keys)	Yw 51100	Y, US
cynophallophora L.	G. Stevenson *s.n.*	U.S.A. (Fla. Keys)	USw 30299	US
cynophallophora L.	P. B. Tomlinson 19.III.62A	U.S.A. (Fla.)	USw 30301	US
crotonantha Standl.	G. P. Cooper 660	Panama	Yw 12293	Y
decidua (Forsk.) Edgew.	Conserv. Forests Punjab *s.n.*	India	Yw 844	
ferruginea L.	G. C. Bucher 4	Cuba	Yw 15999	Y
flexuosa (L.) L.	J. G. Jack 5633	Cuba	Yw 16629	Y, A
flexuosa (L.) L.	W. L. Stern & G. K. Brizicky 236	U.S.A. (Fla. Keys)	Yw 51079	Y, US
flexuosa (L.) L.	G. Stevenson *s.n.*	U.S.A. (Fla. Keys)	USw 30300	US
flexuosa (L.) L.	P. B. Tomlinson 18.III.62A	U.S.A. (Fla.)	USw 30302	US
galeata Fresew.	M. Chudnoff *s.n.*	Israel	USw 18238	Ilanoth 85
linearis Jacq.	H. M. Curran & M. Haman 424	Venezuela	Yw 2797	US, GH
magnifica Gilg ex Ule	B. A. Krukoff 5788	Brazil	USw 9803	NY
nitida Ruiz & Pav.	Ll. Williams 5725	Peru	Yw 18819	US, F
nobilis F. Muell.	"Commercial sample"	Australia	Yw 19327	
odoratissima Jacq.	H. M. Curran & M. Haman 500	Venezuela	Yw 2814	US

TABLE 1.—*Specimens of* Capparis *wood examined*—Continued

Species and Authority	*Collector and No.*	*Country of Origin*	*Wood Collection Catalog No.*	*Location of Vouchers*
odoratissima Jacq.	Espina & Giacometto B9–A	Colombia	Yw 20991	Y
odoratissima Jacq.	G. Newhall & H. Pittier 11	Venezuela	Yw 19929	Y
oxysepala C. Wright ex Radlk.	R. S. Flores (FM 613234)	Mexico	Yw 21317	F
portoricensis Urban	N. L. Britton & W. Kramer XVII	Puerto Rico	Yw 3090	Y
pulcherrima Jacq.	A. Dugand 495; 159	Colombia	Yw 23936	Y
quina Macbr.	Ll. Williams 5753	Peru	Yw 18826	F, US
schunkei Macbr.	Ll. Williams 4118	Peru	Yw 18378	F, US
schunkei Macbr.	Ll. Williams 4820	Peru	Yw 18588	F, US
schunkei Macbr.	Ll. Williams 6692	Peru	Yw 19045	F
sola Macbr.	F. Woytkowski 5826	Peru	USw 18268	MO
tarapotensis Eichl.	Ll. Williams 6654	Peru	Yw 19028	F, US
tenuisiliqua Jacq.	S. J. Record 80	Colombia	Yw 16479	Y, GH
tenuisiliqua Jacq.	S. J. Record 69	Colombia	Yw 16468	Y, GH
verrucosa Jacq.	S. J. Record 44	Colombia	Yw 16443	Y, A
verrucosa Jacq.	S. J. Record 68	Colombia	Yw 16467	Y
verrucosa Jacq.	S. J. Record 82	Colombia	Yw 16481	Y, A, GH
sp.	B. A. Krukoff 6184	Brazil	USw 7539	NY
sp.	P. B. Tomlinson 19.III.62B	U.S.A. (Fla.)	USw 30303	US

TABLE 2.—*Anatomical subdivision of* Capparis *based on ray structure*

Pax & Hoffmann Section	*Species*	*Ray Type*
Capparis ("Eucapparis")	galeata	II
Cynophalla	cynophallophora	I
	flexuosa	I
	tarapotensis	II
	nitida	II
	verrucosa	I
	portoricensis	II
	linearis	I
Mesocapparis	crotonantha	II
Homback	decidua	II
Capparidastrum	tenuisiliqua	I
	oxysepala	I
	baducca	I
	quina	I
	sola	I
Quadrella	odoratissima	I
Colicodendron	schunkei	II
	angulata	II
Calanthea	ferruginea	I
	pulcherrima	I
Busbeckia	nobilis	II

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SYSTEMATIC ANATOMY AND ONTOGENY OF THE STEM IN PASSIFLORACEAE

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SYSTEMATIC ANATOMY AND ONTOGENY OF THE STEM IN PASSIFLORACEAE

By Edward S. Ayensu and William L. Stern[1]

Although the taxonomy of the passionflower family, Passifloraceae, has been studied extensively, especially that of the genus *Passiflora* (Killip 1938), the anatomy and ontogeny of the woody stem have been little explored. This was clearly pointed out by the studies of Stern and Brizicky (1958), who recorded for the first time in the family the presence of anomalous stem growth and storied structure in the xylem of *Passiflora multiflora* L. Interestingly, the occurrence of these two phenomena seemed to accord with Killip's suggestion that *P. multiflora*, the single member of his subgenus *Apodogyne*, ought to be segregated as a separate genus on the basis of its sessile ovary. Obaton (1960) encountered anomalous stems in *Adenia cissampeloides* Harms (included phloem; i.e., phloem strands surrounded by xylem), and *Crossostemma laurifolium* Planch. (intruded phloem; i.e., ribs or flanges of phloem extending into the xylem cylinder from the bark side of the stem) of the Passifloraceae. Her observations indicate that certain other species of *Adenia* (e.g., *Adenia lobata* Engl.) have normal stem structure, even in the thickest portions. She felt compelled, therefore, to segregate as a distinct species a specimen of *Adenia lobata*, obtained from Bingerville, Ivory Coast, which showed abnormal stem structure. Furthermore, she asserts that *Adenia kontiensis* A. Chev., which has long been confused with *Adenia lobata*, is distinguished from it by the less numerous, thicker, and more rounded tubercles on the stem. Because Obaton's study of stem structure in Passifloraceae lacks detailed anatomical descriptions and specimens are not documented by herbarium voucher citation, it is of little use taxonomically.

Except for the works of Stern and Brizicky, and Obaton, there is no record in the anatomical literature that anomalous stem growth occurs in the Passifloraceae. Schenck (1893) states that growth in the stem of Passifloraceae is normal; Solereder (1908) emphasizes that even the climbing forms of Passifloraceae have normal structure. Solereder, furthermore, repudiates Schwendener's (1874) assertion that *Passiflora*

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trifasciata has 6 medullary vascular bundles which are provided on the inside and the outside with small bast-coverings (bicollateral) for the protection of the conducting cells. Dr. L. Chalk of Oxford University, in an informal communication, suggested that Schwendener's remarks at least imply that he suspected the occurrence of anomalous structure in this particular species of *Passiflora*. Neither Metcalfe and Chalk (1950) nor Boureau (1957) make mention of this feature in Passifloraceae.

In the taxonomic studies of Passifloraceae by Harms (1925), Masters (1871), and Killip (1938), no mention of atypical stem development in this family has been noted. Ordinarily, development of the anomalous configuration commences in the thicker portions of the stem, not regularly collected for herbarium specimens. Because of this condition, taxonomists have perhaps overlooked these strange stems.

Owing to certain similarities in the anatomy and morphology of Passifloraceae and Flacourtiaceae, taxonomists have found it difficult to decide to which the genus *Paropsia* should be assigned. Bentham and Hooker (1867) included under Passifloreae, the genera *Passiflora, Tacsonia, Deidamia, Basanthe, Tryphostemma, Paropsia, Smeathmannia, Barteria,* and *Crossostemma.* Harms (1893) later transferred *Paropsia* to Flacourtiaceae, and Gilg (1925) included the genera *Paropsia, Soyauxia, Hounea, Smeathmannia, Paropsiopsis,* and *Barteria* under the tribe *Paropsieae* of this same family. Fernandes and Fernandes (1958a, 1958b) disagree with Harms and Gilg and assert that *Paropsia* should be placed in Passifloraceae. Brizicky (1961) pointed out that the present delimitations of the family seem to be fairly natural. However, he remarked that a taxonomic re-evaluation of Passifloraceae and their closest allies, such as Flacourtiaceae—*Paropsieae,* based on comparative anatomy and other botanical disciplines, is needed.

In a preliminary report on the woods of Flacourtiaceae, Tupper (1934) indicated that axial parenchyma is generally lacking. However, he encountered abundant axial wood parenchyma in the genus *Paropsia* in support of den Berger's (1928) observation that this genus has abundant, diffuse wood parenchyma. Metcalfe and Chalk (1950) mention that although there are certain anatomical differences between *Paropsia* and the genera of Passifloraceae, there are also anatomical similarities, and, for example, the occurrence of fibriform vessel members in some species may support its affinity with Passifloraceae.

Palynological studies by Erdtman (1952) have shown that pollen grains of *Paropsia* are more similar to those of Passifloraceae than to those of Flacourtiaceae. The pollen grains of *Paropsia brazzeana,* for instance, are usually 6-colporate and subprolate; the sexine is as thick

as the nexine, and reticulate. Erdtman suggests that the tribe *Paropsieae* (Flacourtiaceae) should, at least in part, be referred to Passifloraceae.

In general, our investigations uphold the anatomical findings of Tupper and den Berger, and support Bentham and Hooker (1867), and Fernandes and Fernandes (1958a, 1958b) in their assertions that the genus *Paropsia* belongs with Passifloraceae.

Passifloraceae consists of 12 genera with over 500 species distributed throughout the tropics. Eight of the genera are confined to the Old World, three are exclusively American and one, *Passiflora*, is predominantly New World. Most of the Old World genera have few species; more than two-thirds of all species in the family belong to *Passiflora*.

Members of the Passifloraceae (figs. 1, 2) are herbaceous or woody, tendril bearing lianas, or erect shrubs and trees. Leaves are alternate, simple or compound, and have entire, toothed, or deeply cleft margins, with predominantly 3–5 nerved blades. Petioles are often glandulif-erous; stipules are setaceous or broadly ovate, but sometimes foliaceous.

Flowers may be brilliantly colored or greenish, many centimeters in diameter or less than one. They may be axillary or in cymes, but are usually reduced to solitary or paired peduncles. Bracts are ordinarily present. Five (4), rarely 3, basally connate sepals are present. The petals 5(4), or wanting, are distinct or briefly basally connate, often smaller than the sepals. Sepals and petals are imbricate. The floral tube is usually associated with a corona. The androecium consists of 5 stamens, rarely 10, usually opposite the petals; anthers are versatile, 2-locular at anthesis, and dehisce longitudinally. The gynoecium consists of 3–5 carpels; stigmatic branches are capitate, clavate, or discoid; the styles number as many as the carpels; the ovary is stipitate, rarely sessile, 1-locular with numerous anatropous ovules on 3–5 parietal placentae. The fruit is a berry or a loculicidal capsule; the seed has a straight embryo and fleshy endosperm. Both Killip (1938) and Masters (1871) have excellent descriptions of these highly modified flowers, accompanied by drawings and explanations.

Materials and Methods

Table 1 lists the 60 stem and wood specimens (44 species of 9 genera) examined. The citation of specimens follows the recommendations of Stern and Chambers (1960), and herbarium vouchers are listed as well as the names and numbers of the collectors. Names of species are in accordance with those stated in Killip (1938) for American Passifloraceae.

Microtechnical procedures followed were modified from those outlined by Wetmore (1932) and are standard for the preparation of sections of stem and wood. Microscope slides of wood specimens prepared for this investigation have been deposited in the Division of Plant Anatomy of the Smithsonian Institution (USw).

Diagnostic characters for descriptions of passifloraceous woods were selected from Tippo's (1941) list. For the most part, terms used in the anatomical descriptions comply with those approved by the Committee on Nomenclature of the International Association of Wood Anatomists (1957). In a few instances, however, certain liberties were taken with the definitions.

Lack of sufficient wood material in a number of cases made the preparation of macerations impracticable, hence, length measurements of fibers and vessel elements were taken from sections. Therefore, our method of making measurements cannot conform exactly to the recommendations of Chalk and Chattaway (1934, 1935) that total lengths of cells be used. Tangential vessel diameters and lengths of fibers and vessel elements were recorded from 30 cells in each specimen.

Because of the conflicting and ambiguous results brought on by employing only names to categorize vascular rays (Kribs 1935), it was thought best to employ the suggestions of the Committee on Nomenclature (1957). These direct the anatomist to describe rays using brief sentences or phrases to point out the width, height, frequency of occurrence, and cellular composition. Classification of axial wood parenchyma used here is in most part that presented by Metcalfe and Chalk (1950). The various types of parenchyma distribution fall into two main categories: apotracheal, in which parenchyma strands show no regular relation to vessels; and paratracheal, in which parenchyma strands show a close and regular association with vessels.

Four descriptive terms have been chosen to characterize the appearance on the transverse surface of the mature vascular cylinder of stems in Passifloraceae: (1) NORMAL TYPE—a stem in which xylem and phloem cylinders are roughly circular and concentric with little or no distortion of pith and cortex; (2) INCLUDED PHLOEM TYPE—similar to (1), but with patches of phloem embedded in the xylem cylinder; (3) INTERRUPTED TYPE—wedge-shaped sections of xylem, alternating around the stem with similarly shaped sections of phloem, characterized by marginal series of steps; (4) DISPERSED TYPE—irregularly shaped, disoriented strands of xylem and phloem associated with fragments of vascular cambium spread throughout a parenchymatous matrix.

TABLE 1.—*Specimens of Passifloraceae stems examined*

Citation of specimens follows the recommendations of Stern and Chambers (1960). WOOD COLLECTIONS: (Yw) The Samuel James Record Memorial Collection, Yale University, New Haven; (USw) Division of Plant Anatomy, Smithsonian Institution, Washington; (Aw) The Arnold Arboretum, Cambridge; (Uw) Botanical Museum and Herbarium, Utrecht. HERBARIA: (TEF) Inspection Générale des Eaux et Forêts, Tananarive; (FHO) The Imperial Forestry Institute, Oxford; (Y) Yale School of Forestry, New Haven; (A) The Arnold Arboretum, Cambridge; (US) U.S. National Herbarium, Smithsonian Institution, Washington; (NY) New York Botanical Garden, New York; (U) Botanical Museum and Herbarium, Utrecht; (K) Royal Botanic Gardens, Kew.]

Species	*Collector and Number*	*Geographical Origin*	*Herbarium Voucher*	*Location and Catalog Number*
Adenia lobata (Jacq.) Engl.	E. S. Ayensu *s.n.*	Ghana	US	
Androsiphonia adenostegia Stapf	G. P. Cooper 276	Liberia	Y	Yw 15191
Barteria nigritiana Hook. f.	E. S. Ayensu *s.n.*	Ghana	US	
Crossostemma laurifolium Planch.	C. Vigne 3503	Ghana	FHO	Yw 29724
Dilkea johannesii Rodr.	A. Ducke 329	Brazil	Y	Yw 34093
Mitostemma glaziovii Mast.	A. C. Smith 3117	British Guiana	Y	Yw 35812
Paropsia adenostegia (Stapf) Engl.	G. P. Cooper 211	Liberia	Y	Yw 15140
Paropsia madagascariensis (Baill.) H. Perrier	—	Madagascar	TEF	USw 27402
Paropsia schliebenii Sleumer	H. J. Schlieben 429 (5442)	Tanganyika	Y	Yw 30003
Paropsia vareciformis Mast.	H. E. Desch 2003 (32695)	Malaya	—	Yw 29187
Passiflora arborea Spreng.	J. Cuatrecasas 22014	Colombia	Y	Yw 44493
Passiflora auriculata H.B.K.	R. H. Woodworth & P. A. Vestal 362	Panama Canal Zone	A	Aw 362
Passiflora auriculata H.B.K.	W. L. Stern 1585A	Trinidad	US	USw 30687
Passiflora coccinea Aubl.	B. Maguire 24179	Suriname	NY	Yw 44096
Passiflora caerulea L.	—	—	—	Aw 5323
Passiflora coriacea A. Rich.	R. H. Woodworth & P.A. Vestal 501	Panama Canal Zone	A	Aw 501
Passiflora edulis Sims	—	Cuba (cult. Soledad)	—	Aw 5283
Passiflora edulis Sims	E. S. Ayensu *s.n.*	Ghana	US	
Passiflora edulis Sims	W. L. Stern & S. Carlquist 1287	Kauai, Hawaii	US	USw 25985

TABLE 1.—*Specimens of Passifloraceae stems examined*—Continued

Species	*Collector and Number*	*Geographical Origin*	*Herbarium Voucher*	*Location and Catalog Number*
Passiflora elliptica Gardn.	H. S. Irwin 2222	Brazil	Y	Yw 53094
Passiflora fuchsiiflora Hemsl.	F. P. Jonker & Daniels 817	Suriname	U	USw 30677
Passiflora fuchsiiflora Hemsl.	F. P. Jonker & Daniels 1098	Suriname	U	USw 30678
Passiflora fuchsiiflora Hemsl.	J. Lanjouw & J. C. Lindeman 2639	Suriname	U	Uw 1859, USw 30686
Passiflora fuchsiiflora Hemsl.	B. Maguire & D. B. Fanshawe 22807	British Guiana	NY	Yw 43907
Passiflora gigantifolia Harms (?)	A. Rimbach 50	Ecuador	Y	Yw 20743
Passiflora glandulosa Cav.	A. C. Smith 2822	British Guiana	Y	Yw 35711
Passiflora glandulosa Cav.	BAFOG 4033	French Guiana	U	USw 30679
Passiflora glandulosa Cav.	F. P. Jonker & Daniels 788	Suriname	U	USw 30680
Passiflora glandulosa Cav.	F. P. Jonker & Daniels 830	Suriname	U	USw 30681
Passiflora glandulosa Cav.	J. Lanjouw & C. J. Lindeman 1820	Suriname	U	Uw 1559, USw 30685
Passiflora glandulosa Cav.	J. Lanjouw & J. C. Lindeman 2765	Suriname	U	USw 30682
Passiflora glandulosa Cav.	J. C. Lindman 4530	Suriname	U	Uw 3142
Passiflora glandulosa Cav.	A. A. Pulle 353	Suriname	U	USw 30683
Passiflora laurifolia L.	—	Cuba	A	Aw 25273
Passiflora maguirei Killip	B. Maguire & D. B. Fanshawe 23285	British Guiana	US	Yw 44006
Passiflora maliformis Vell.	—	Cuba (cult. Soledad)	—	Aw 5284
Passiflora menispermifolia H. B. K.	R. H. Woodworth & P. A. Vestal 637	Panama Canal Zone	A	Aw 637

TABLE 1.—*Specimens of Passifloraceae stems examined*—Continued

Species	*Collector and Number*	*Geographical Origin*	*Herbarium Voucher*	*Location and Catalog Number*
Passiflora misera H.B.K.	R. H. Woodworth & P. A. Vestal 456	Panama Canal Zone	A	Aw 456
Passiflora mollissima (H.B.K.) Bailey = Tacsonia mollissima H.B.K.	A. Rimbach 19	Ecuador	Y	Yw 19485
Passiflora multiflora L.	W. L. Stern & G. K. Brizicky 522	Plantation Key, Florida	Y	Yw 51303
Passiflora nitida H.B.K.	J. J. Wurdack & L. S. Adderley 43025	Venezuela	NY	USw 17808
Passiflora punctata L.	R. H. Wetmore & E. Abbe 26	Panama Canal Zone	A	Aw 26
Passiflora quadrangularis L.	M. Grant 2617	Tahiti	Y	Yw 26455
Passiflora quadriglandulosa Radscheid	G. H. M. Lawrence 607	Colombia	A	Aw 21303
Passiflora riparia Mart. ex Mast.	A. C. Smith 3157	British Guiana	Y	Yw 35837
Passiflora rubra L.	—	—	—	Aw 5286
Passiflora securiclata Mast.	A. C. Smith 3116	British Guiana	Y	Yw 35811
Passiflora seemannii Griseb.	R. H. Wetmore & E. Abbe 147	Panama Canal Zone	A	Aw 147
Passiflora spinosa (Poepp. & Endl.) Mast.	J. J. Wurdack & L. S. Adderley 43009	Venezuela	NY	USw 17798
Passiflora variolata Poepp. & Endl.	J. J. Wurdack & L. S. Adderley 43230	Venezuela	NY	USw 17923
Passiflora vitifolia H.B.K.	R. H. Wetmore & R. H. Woodworth *s.n.*	Panama Canal Zone	—	Aw 854A
Passiflora vitifolia H.B.K.	J. J. Wurdack & L. S. Adderley 43026	Venezuela	NY	USw 17809
Passiflora vitifolia H.B.K.	F. Woytkowski 509	Peru	Y	Yw 52812

TABLE 1.—*Specimens of Passifloraceae stems examined*—Continued

Species	*Collector and Number*	*Geographical Origin*	*Herbarium Voucher*	*Location and Catalog Number*
Passiflora sp. nov.	J. J. Wurdack & L. S. Adderley 43154	Venezuela	NY	USw 17874
Passiflora sp.	B. Maguire 28327	Venezuela	NY	USw 24782
Passiflora sp.	J. J. Wurdack & L. S. Adderley 43055	Venezuela	NY	USw 17834
Passiflora sp.	F. P. Jonker & Daniels 1227	Suriname	U	USw 30684
Smeathmannia laevigata Sol. ex R. Br.	J. Espirito-Santo *s.n.*	Portuguese Guinea	US	USw 30675
Smeathmannia pubescens Sol. ex R. Br.	G. P. Cooper 442	Liberia	Y	USw 5792
Smeathmannia pubescens Sol. ex R. Br.	G. P. Cooper 51	Liberia	K	Yw 13701

Anatomy of the Family

Growth rings are absent in most of the species investigated except for *Paropsia schliebenii* and *Smeathmannia pubescens*. All of the woods are diffuse-porous, the randomly distributed pores ranging in size from very small to moderately large. The occurrence of solitary pores (figs. 3–6) characterizes the wood of Passifloraceae, although radial (figs. 7–9) and tangential multiples (fig. 4), as well as pore clusters, are found in some species. Pores in all species are rounded; however, "flattened" pores (fig. 3) sometimes appear. Pores are variable in size even in different species of the same genus. In some species of *Passiflora*, for example, vessel diameter is less than 100 μ, while in other species the vessel diameter is over 300 μ. Vessel element lengths are extremely short in *Adenia* and *Passiflora* to moderately short in *Crossostemma* and *Smeathmannia*.

Slope of the end walls in the vessel elements varies from oblique (fig. 14) to transverse. Oblique end walls are regularly associated with wood from arboreal species. Perforation plates are almost exclusively simple (fig. 11); in *Paropsia adenostegia*, both simple and scalariform perforation plates (fig. 12) may occur in the same section. The scalariform plates here have few bars, and at times show a tendency toward the reticulate configuration. Metcalfe and Chalk (1950) observed a few scalariform plates in *Androsiphonia* and *Mitostemma glaziovii*, but none was observed in *M. glaziovii* during this investigation.

The imperforate tracheary elements generally consist of fiber-tracheids (fig. 13) bearing pits with very distinct borders. However, tracheids (fig. 13) occur in some species, and very thick-walled libriform wood fibers (fig. 10) are commonly found in the arboreal members of the family. The fiber lengths range from moderately short to medium-sized.

Intervascular pitting is mostly alternate (fig. 21), and the pit apertures are generally elliptical or flattened, and tend to be limited by the border. In *Passiflora fuchsiiflora* coalesced apertures were observed.

Fibriform vessel members (fig. 13) of Woodworth (1935) were observed in most species of *Passiflora* and in *Paropsia schliebenii.* These cells are longer than vessel elements in the same species, and bear simple perforation plates that occur about one-fourth the distance from each end of the element. Fibriform vessel members are fusiform cells more or less randomly distributed within the groundmass, and show fewer axial connections among conspecific elements than occur among elements making up typical vessels. Lateral wall pitting of these cells is similar to that of the fiber-tracheids.

Vascular ray tissue (figs. 10, 17) is composed of both uniseriate and multiseriate rays. Some species have typically high multiseriate rays; in others, only biseriate rays with long uniseriate wings occur. The tendency for rays to widen centrifugally, as seen in transverse sections, is common in *Passiflora.* In most species of *Passiflora* storied uniseriate rays (fig. 17) are found among higher, nonstoried multiseriate rays. Vascular rays may be heterocellular or homocellular. In *Paropsia vareciformis* rays consist of procumbent cells associated with uniseriate margins of square cells. Rays consist exclusively of upright cells in *Passiflora maguirei* and *Passiflora mollissima.* Ontogenetic splitting of multiseriate rays into uniseriate and biseriate rays was observed in many species. Chalk and Chattaway (1933) reported on the presence of perforated ray cells in *Androsiphonia adenostegia.* Similarly perforated ray cells were observed in *Passiflora vitifolia* and *Passiflora elliptica* (fig. 15).

Axial wood parenchyma is generally moderately abundant to very abundant. The usual arrangement is apotracheal (figs. 7, 8, 20); however, paratracheal parenchyma (figs. 3–6, 9) does occur, and in some species it is vasicentric and aliform. Combinations of diffuse and diffuse-in-aggregates, with a tendency toward banded, and even vasicentric arrangements are found in the same species (fig. 9); narrow bands occur in others. In *Paropsia,* the bands are wavy; banded and aliform arrangements are both observed in *Dilkea johannesii;* in *Crossostemma laurifolium,* only vasicentric parenchyma arrangement occurs.

Pith flecks (fig. 16) occur in the wood of about 70 percent of the *Passiflora* species studied. Three types of anomalous stem development (see pp. 48, 60, 61) were observed in the species investigated: included phloem type, interrupted type (figs. 24, 25), and dispersed type (fig. 23). Tyloses and gummy deposits were present in ray cells and vessels (fig. 8) of a few species. Rhomboidal crystals, and occasionally druses, were observed in most species investigated, particularly in ray cells.

Anatomy of the Species

Crossostemma laurifolium: Growth rings absent; pores mainly solitary, rounded, average diameter 198 μ, range 140 μ–210 μ; average vessel element length 424 μ, range 311 μ–442 μ; vessel wall thickness 2 μ–5 μ; perforation plates simple; vessel element end wall inclination almost transverse; intervascular pitting opposite to alternate; imperforate tracheary elements fiber-tracheids, average length 614 μ, range 497 μ–756 μ; fibriform vessel members absent; vascular rays mostly multiseriate without any uniseriate extensions, 2–5 cells wide, 8–12 cells high, few uniseriate, 5–14 cells high, mainly homocellular consisting of procumbent cells, uniseriates sometimes showing upright cells; axial parenchyma vasicentric; crystals present in ray cells; uniseriate rays vaguely storied; stem anomalous (interrupted); pith flecks absent.

Dilkea johannesii: Growth rings absent; pores mostly solitary, rounded, average diameter 205 μ, range 104 μ–211 μ; average vessel element length 378 μ, range 335 μ–401 μ; vessel wall thickness 4 μ–8μ; perforation plates simple; vessel element end wall inclination transverse; intervascular pitting alternate; imperforate tracheary elements fiber-tracheids, average length 560 μ, range 433 μ–741 μ; fibriform vessel members absent; vascular rays mostly multiseriate without any uniseriate extensions, 2–6 cells wide, 5–13 cells high, some uniseriate, 4–15 cells high, mainly heterocellular; axial parenchyma diffuse, abundant; crystals present in ray cells; uniseriate rays vaguely storied; stem normal; pith flecks absent.

Mitostemma glaziovii: Growth rings absent; pores mostly solitary, rounded, average diameter 112 μ, range 92 μ–130 μ; average vessel element length 416 μ, range 392 μ–478 μ; vessel wall thickness 3 μ–5 μ; perforation plates simple; vessel element end wall inclination transverse; intervascular pitting alternate; imperforate tracheary elements fiber-tracheids, average length 550 μ, range 520 μ–719 μ; fibriform vessel members absent; vascular rays mostly multiseriate without any uniseriate extensions, 2–4 cells wide, 7–12 cells high, few uniseriate, 8–13 cells high, heterocellular; axial parenchyma diffuse; crystals present in ray cells; storying absent; stem normal; pith flecks absent.

Paropsia adenostegia: Growth rings inconspicuous; pores mainly solitary, few radial multiples, angular to rounded, average diameter 50 μ, range 35 μ–56 μ; average vessel element length 450 μ, range 420 μ–773 μ; vessel wall thickness 2 μ–3 μ; perforation plates scalariform and simple; vessel element end wall inclination oblique; intervascular pitting alternate; imperforate tracheary elements libriform wood fibers, average length 668 μ, range 574 μ–968 μ; fibriform vessel members absent; vascular rays mainly uniseriate, 5–12 cells high, and biseriate, 5–12 cells high, heterocellular; axial parenchyma diffuse, banded in places; crystals absent; storying absent; stem normal; pith flecks absent.

Paropsia madagascariensis: Growth rings absent; pores mainly in radial multiples, rounded, average diameter 85 μ, range 64 μ–127 μ; average vessel element length 468 μ, range 420 μ–780 μ; vessel wall thickness 2 μ–3 μ; perforation plates simple; vessel element end wall inclination oblique to transverse; intervascular pitting alternate; imperforate tracheary elements libriform wood fibers, average length 580 μ, range 394 μ–803 μ; fibriform vessel members absent; vascular rays multiseriate without any uniseriate extensions, 2–3 cells wide, 5–11 cells high, heterocellular; axial parenchyma diffuse; crystals present in ray cells; storying absent; stem normal; pith flecks absent.

Paropsia schliebenii: Growth rings present; pores mainly in radial multiples, rounded, average diameter 45 μ, range 27 μ–62 μ; average vessel element length 590 μ, range 398 μ–772 μ; vessel wall thickness 2 μ–3 μ; perforation plates simple; vessel element end wall inclination oblique to transverse; intervascular pitting alternate; imperforate tracheary elements libriform wood fibers, average length 775 μ, range 424 μ–907 μ; fibriform vessel members present; vascular rays multiseriate, 2–3 cells wide, 13–28 cells high, few with uniseriate wings 4–8 cells high, largely homocellular, cells mainly procumbent but with a few upright cells; axial parenchyma diffuse; crystals absent; uniseriate rays vaguely storied; stem normal; pith flecks absent.

Paropsia vareciformis: Growth rings inconspicuous; pores mainly in radial multiples, rounded, average diameter 70 μ, range 62 μ–110 μ; average vessel element length 480 μ, range 382 μ–697 μ; vessel wall thickness 2 μ–3 μ; perforation plates simple; vessel element end wall inclination almost transverse; intervascular pitting alternate; imperforate tracheary elements fiber-tracheids and libriform wood fibers, average length 668 μ, range 511 μ–939 μ; fibriform vessel members absent; vascular rays multiseriate 2–3 cells wide, 18–34 cells high, few with uniseriate wings 4–8 cells high, mainly homocellular, consisting solely of procumbent cells, other rays with some upright cells; axial parenchyma diffuse; crystals present in ray cells; uniseriate rays storied in places; stem normal; pith flecks absent.

Passiflora arborea: Growth rings present; pores 50 percent solitary, 30 percent radial multiples, 20 percent clusters, rounded, average diameter 130 μ, range 98 μ–152 μ; average vessel element length 343 μ, range 295 μ–587 μ; vessel wall thickness 2 μ–3 μ; perforation plates simple; vessel element end wall inclination oblique to transverse; intervascular pitting alternate; imperforate tracheary elements fiber-tracheids and libriform wood fibers, average length 481 μ, range 394 μ–647 μ; fibriform vessel members absent; vascular rays biseriate with long uniseriate wings 9–22 cells high, heterocellular; axial parenchyma mostly diffuse, diffuse-in-aggregates to banded and vasicentric; storying absent; stem normal; pith flecks present.

Passiflora auriculata: Growth rings absent; pores mainly solitary, rounded, average diameter 210 μ, range 198 μ–230 μ; average vessel element length 362 μ, range 303 μ–479 μ; vessel wall thickness 2 μ–5 μ; perforation plates simple; vessel element end wall inclination transverse; intervascular pitting opposite to alternate; imperforate tracheary elements fiber-tracheids, average length 472 μ, range 403 μ–723 μ; fibriform vessel members present; vascular rays mainly multiseriate 2–8 cells wide, 7–30 cells high, few with uniseriate wings 4–9 cells high, some uniseriate rays 5–12 cells high, heterocellular; axial parenchyma diffuse; crystals present in ray cells; uniseriate rays storied; stem anomalous (included phloem); pith flecks absent; tyloses present.

Passiflora coccinea: Growth rings absent; pores mainly solitary, rounded, average diameter 210 μ, range 182 μ–231 μ; average vessel element length 385 μ, range 307 μ–478 μ; vessel wall thickness 2 μ–7 μ; perforation plates simple; vessel element end wall inclination oblique to transverse; intervascular pitting alternate; imperforate tracheary elements tracheids and fiber-tracheids, average length 437 μ, range 410 μ–629 μ; fibriform vessel members present; vascular rays mainly uniseriate 1–18 cells high, some multiseriate without any uniseriate extensions, 2–8 cells wide, 6–13 cells high, heterocellular; axial parenchyma diffuse with local banding; crystals absent; uniseriate rays storied; stem anomalous (interrupted); pith flecks present; tyloses present.

Passiflora edulis: Growth rings absent; pores mainly solitary, rounded, average diameter 131 μ, range 101 μ–168 μ; average vessel element length 185 μ, range 143 μ–208 μ; vessel wall thickness 2 μ–7 μ; perforation plates simple; vessel element end wall inclination transverse; intervascular pitting opposite to alternate; imperforate tracheary elements fiber-tracheids, average length 315 μ, range 298 μ–472 μ; fibriform vessel members present; vascular rays mainly uniseriate 1–14 cells high, mostly 6–12 cells high, some multiseriate 2–3 cells wide, 8–12 cells high, uniseriate wings 4–8 cells high, few very high multiseriate rays, heterocellular; axial parenchyma mainly diffuse with some

banding; crystals present in ray cells; uniseriate rays storied; stem anomalous (interrupted); pith flecks absent.

Passiflora elliptica: Growth rings absent; pores 30 percent solitary, 62 percent radial multiples, 8 percent clusters, rounded, average diameter 117 μ, range 96 μ–184 μ; average vessel element length 316 μ, range 299 μ–437 μ; vessel wall thickness 2 μ–5 μ; perforation plates simple; vessel element end wall inclination oblique to transverse; intervascular pitting opposite to alternate; imperforate tracheary elements fiber-tracheids, average length 420 μ, range 413 μ–489 μ; fibriform vessel members present; vascular rays mainly multiseriate without any uniseriate extensions, 2–8 cells wide, 7–12 cells high, few uniseriate 4–9 cells high, heterocellular; axial parenchyma diffuse; crystals absent; uniseriate rays vaguely storied; stem normal; pith flecks present; tyloses present.

Passiflora fuchsiiflora: Growth rings absent; pores mainly solitary, rounded, average diameter 135 μ, range 97 μ–154 μ; average vessel element length 396 μ, range 284 μ–473 μ; vessel wall thickness 2 μ–5 μ; perforation plates simple; vessel element end wall inclination oblique to transverse; intervascular pitting opposite to alternate; imperforate tracheary elements fiber-tracheids, average length 471 μ, range 435 μ–622 μ; fibriform vessel members present; vascular rays mainly multiseriate 2–8 cells wide, 6–13 cells high, uniseriate wings 4–6 cells high, few very high multiseriate rays, some uniseriate 4–8 cells high, heterocellular; axial parenchyma diffuse and diffuse-in-aggregates with a few narrow bands; crystals present in ray cells; uniseriate rays and parenchyma strands vaguely storied; stem normal; pith flecks present.

Passiflora glandulosa: Growth rings vague; pores 60 percent solitary, 40 percent radial multiples, rounded, average diameter 200 μ, range 142 μ–254 μ; average vessel element length 341 μ, range 311 μ–441 μ; vessel wall thickness 2 μ–7 μ; perforation plates simple; vessel element end wall inclination oblique to transverse; intervascular pitting alternate; imperforate tracheary elements fiber-tracheids, average length 403 μ, range 361 μ–547 μ; fibriform vessel members present; vascular rays mainly uniseriate 1–7 cells high, some multiseriate 2–8 cells wide, 4–9 cells high, few very high multiseriate rays, heterocellular; axial parenchyma diffuse and in narrow bands; few crystals present in ray cells; uniseriate rays storied; stem anomalous (interrupted); pith flecks present.

Passiflora laurifolia: Growth rings absent; pores mainly solitary, rounded, average diameter 124 μ, range 98 μ–155 μ; average vessel element length 318 μ, range 264 μ–410 μ; vessel wall thickness 2 μ–5 μ; perforation plates simple; vessel element end wall inclination oblique to transverse; intervascular pitting opposite to alternate; imperforate tracheary elements fiber-tracheids, average length 474 μ, range

401 μ–498 μ; fibriform vessel members present; vascular rays mainly multiseriate 2–5 cells wide, 4–13 cells high, few uniseriate 1–15 cells high, few very high multiseriate rays, homocellular, consisting entirely of upright cells; axial parenchyma diffuse; crystals present in ray cells; uniseriate rays vaguely storied; stem normal; pith flecks present.

Passiflora maguirei: Growth rings absent; pores 85 percent solitary, radial multiples 10 percent, clusters 5 percent, rounded, average diameter 75 μ, range 42 μ–114 μ; average vessel element length 211 μ, range 160 μ–351 μ; vessel wall thickness 2 μ–4 μ; perforation plates simple; vessel element end wall inclination oblique to transverse; intervascular pitting alternate; imperforate tracheary elements fiber-tracheids and libriform wood fibers, average length 488 μ, range 408 μ–730 μ; fibriform vessel members absent; vascular rays mainly uniseriate 1–12 cells high, some multiseriate without uniseriate extensions, 2–8 cells wide, 6–12 cells high, homocellular, composed solely of upright cells; axial parenchyma diffuse, diffuse-in-aggregates, and in narrow bands; crystals absent; uniseriate rays vaguely storied; stem normal; pith flecks absent.

Passiflora mollissima: Growth rings absent; pores 90 percent solitary, 10 percent radial multiples, rounded, average diameter 111 μ, range 92 μ–170 μ; average vessel element length 368 μ, range 284 μ–433 μ; vessel wall thickness 2 μ–5 μ; perforation plates simple; vessel element end wall inclination oblique to transverse; intervascular pitting opposite to alternate; imperforate tracheary elements fiber-tracheids, average length 432 μ, range 401 μ–520 μ; fibriform vessel members present; vascular rays mainly multiseriate without uniseriate extensions, 2–5 cells wide, 6–14 cells high, few uniseriate 1–10 cells high, homocellular, comprising only square cells; ray cells with simple perforations; axial parenchyma diffuse; crystals present in ray cells; uniseriate rays vaguely storied; stem normal; pith flecks absent.

Passiflora multiflora: Growth rings absent; pores mainly solitary, rounded, average diameter 128 μ, range 102 μ–233 μ; average vessel element length 345 μ, range 210 μ–445 μ, vessel wall thickness 2 μ–5 μ; perforation plates simple; vessel element end wall inclination transverse; intervascular pitting alternate; imperforate tracheary elements fiber-tracheids, average length 422 μ, range 354 μ–591 μ; fibriform vessel members present; vascular rays mainly uniseriate 2–15 cells high, some biseriate 25 or more cells high, homocellular, entirely of procumbent cells; axial parenchyma apotracheal and paratracheal; crystals present in ray cells; uniseriate rays storied, fibrous elements somewhat storied; stem anomalous (dispersed); pith flecks absent.

Passiflora nitida: Growth rings absent; pores solitary, rounded, average diameter 138 μ, range 104 μ–157 μ; average vessel element length 234 μ, range 219 μ–447 μ; vessel wall thickness 2 μ–4 μ; vessel

FIG. 1. *Pavonia grandiflora* A. St.-Hil. Flowering specimen. Photographed in cultivation at the Botanical Garden, Washington, D.C. FIG. 2. *Pavonia schiedeana* Steud. Fruiting specimen. Photographed in cultivation at the Botanical Garden, Washington, D.C.

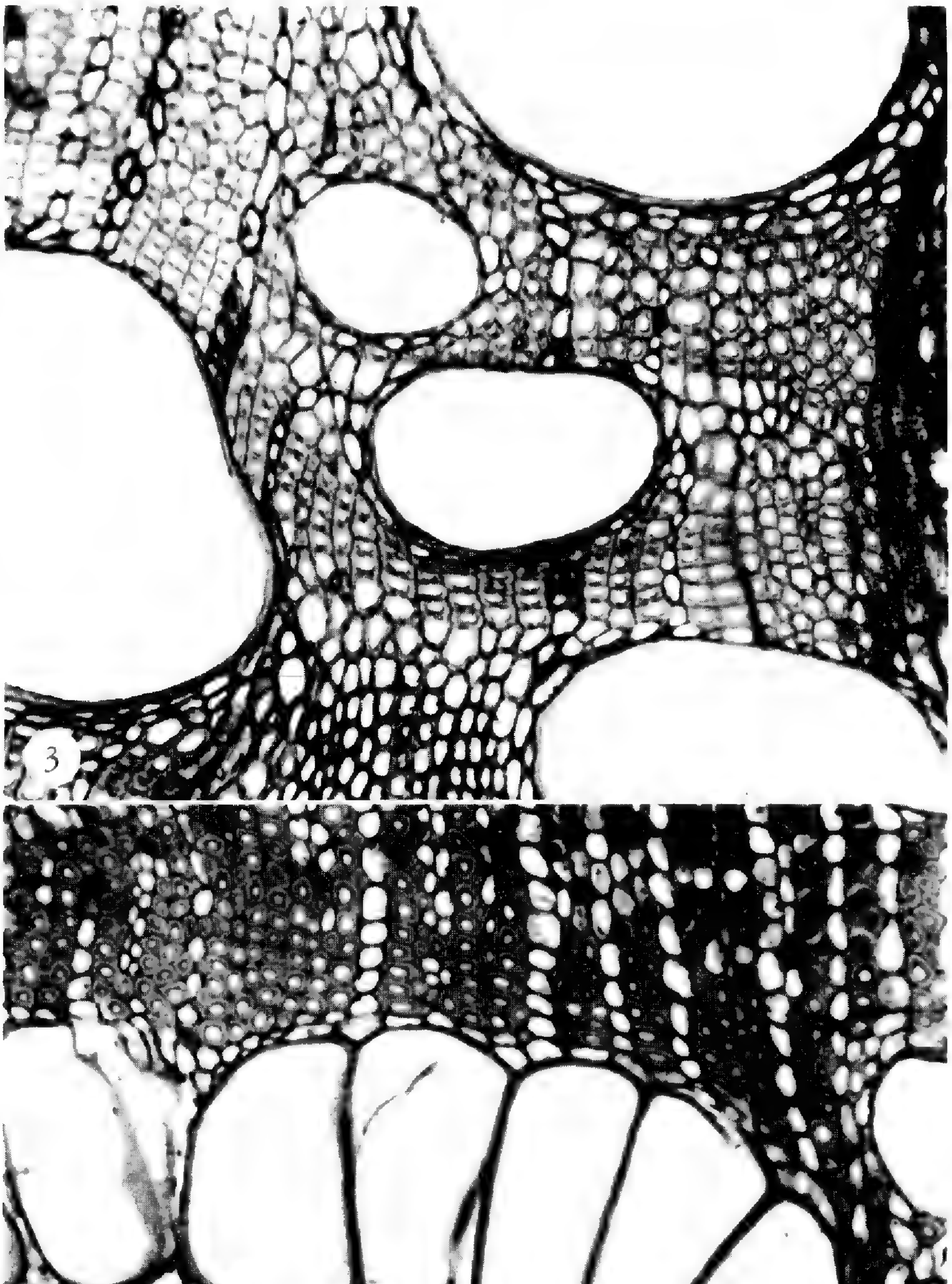


FIG. 3.—*Passiflora coccinea* Aubl. Transverse section of wood showing solitary pores characteristic of lianous stems in Passifloraceae, × 150. FIG. 4.—*Passiflora* sp. *Jonker & Daniels 1227.* Transverse section of wood showing tangential pore disposition and vasicentric parenchyma, × 150.

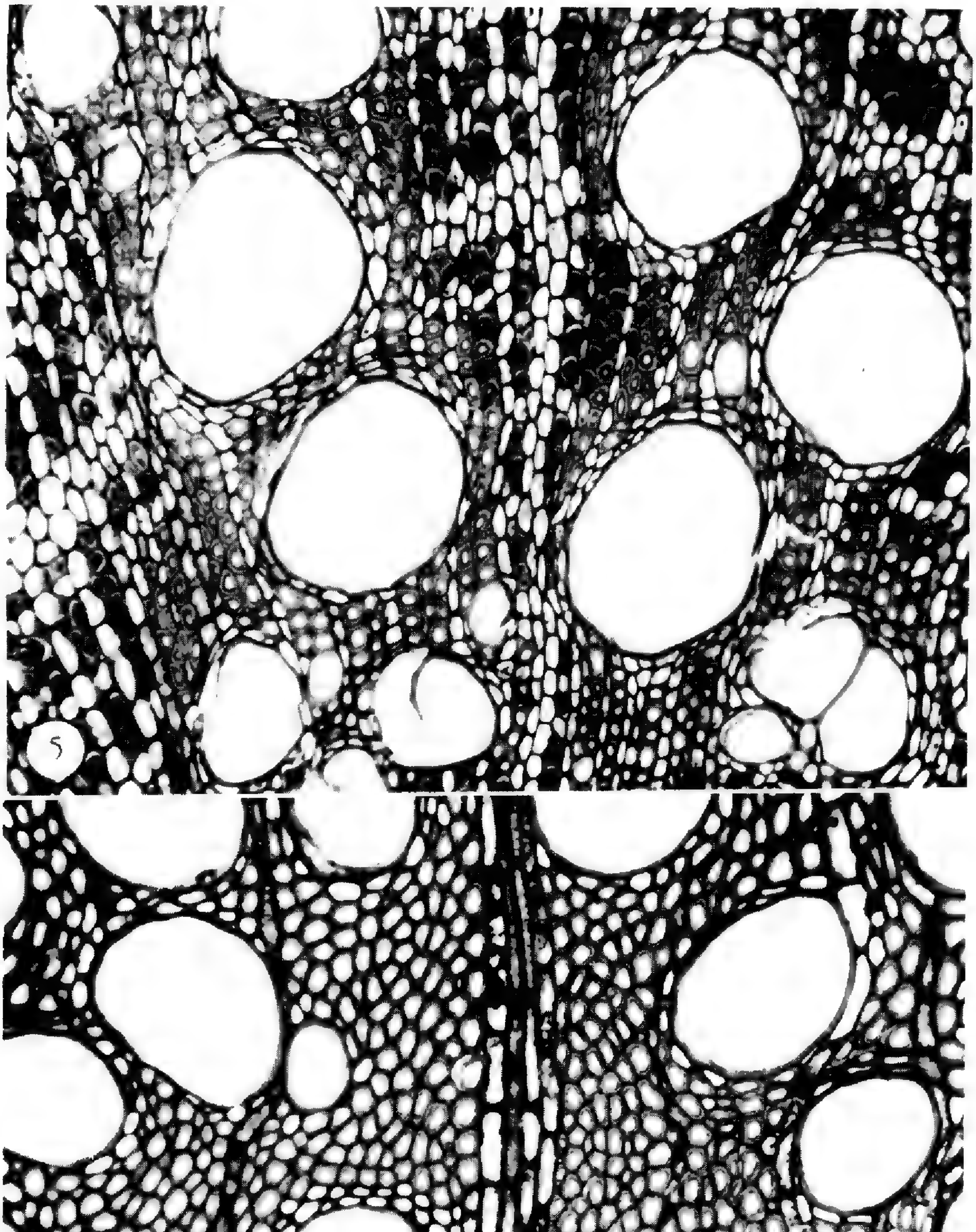


FIG. 5. *Passiflora* sp. *Jonker & Daniels 1227.* Transverse section of wood showing mainly solitary pores, short apotracheal bands and vasicentric axial parenchyma, × 130. FIG. 6—*Crossostemma laurifolium* Planch. Transverse section of wood with vasicentric parenchyma arrangement, and solitary, rounded pores, × 150.

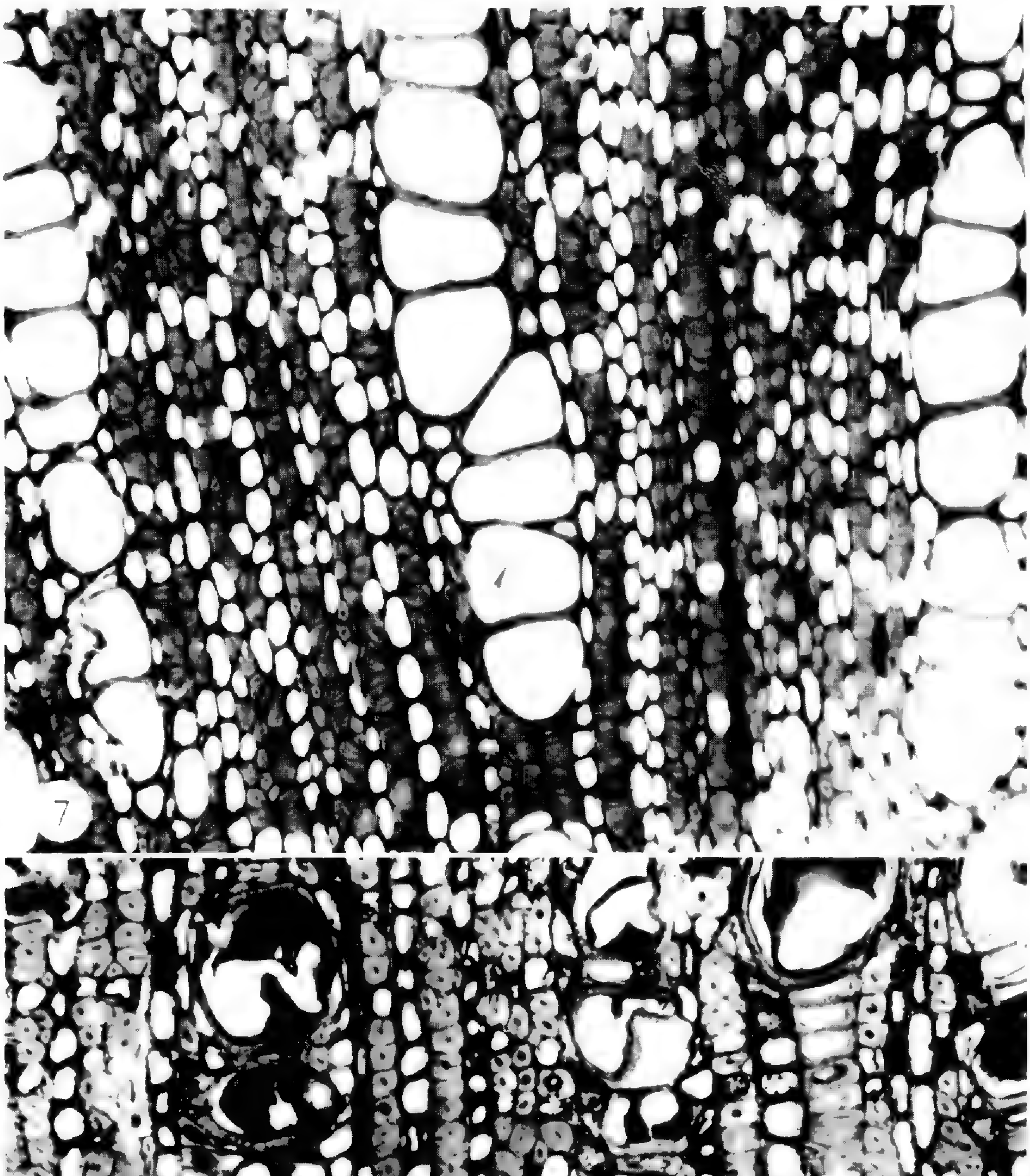


FIG. 7. *Sarcobatus vermiculatus* Sol. ex R. Br. Transverse section of wood showing radial pore multiples characteristic of arborescent stems in Passifloraceae, and diffuse-in aggregates axial parenchyma arrangement. ×150. FIG. 8. *Sarcobatus baileyi* Sol. ex R. Br. Transverse section of xylem showing radial pore multiples, tyloses, and gummy deposits in vessels, axial and ray parenchyma cells. ×160.

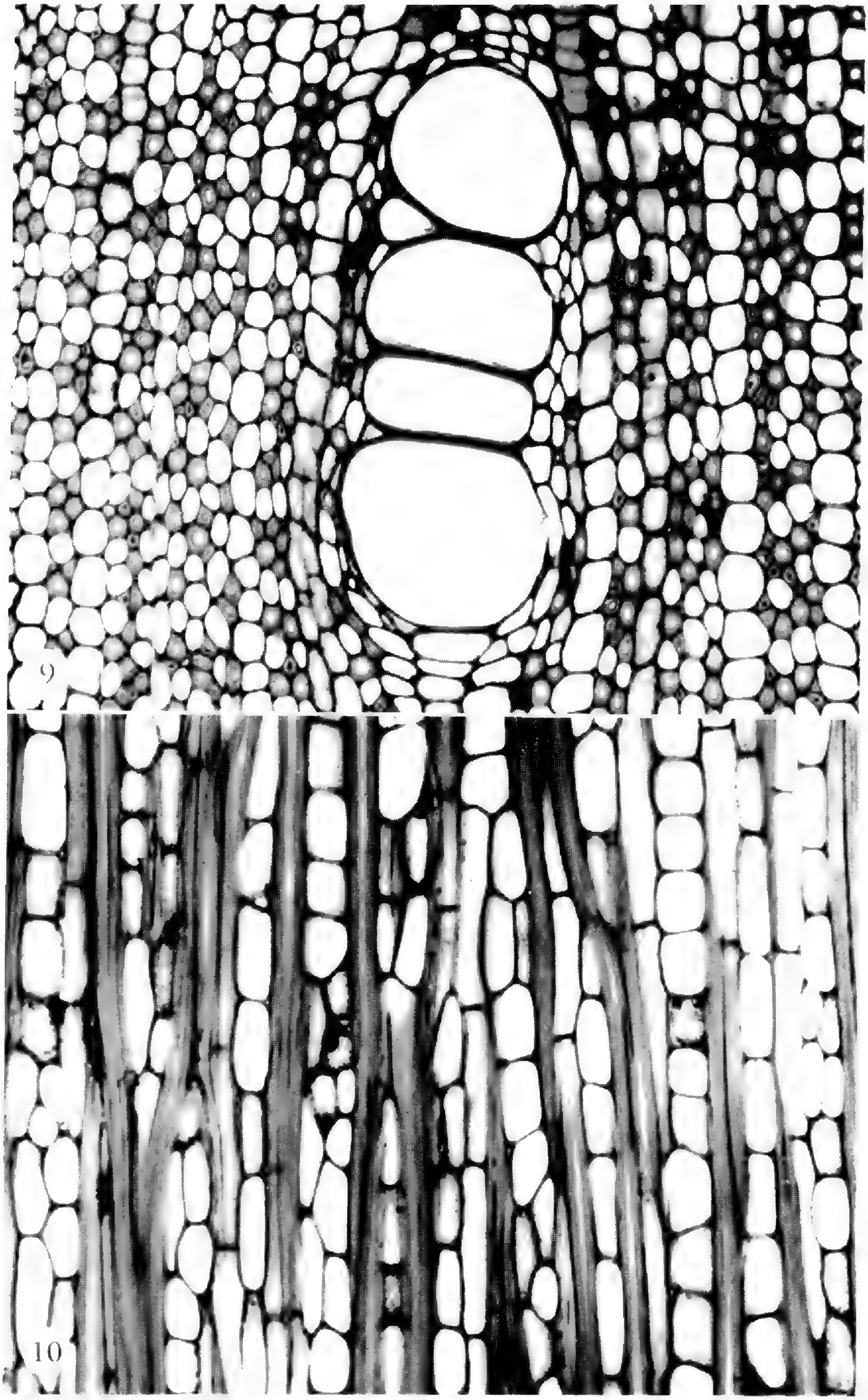


FIG. 9.—*Passiflora arborea* Spreng. Transverse section of wood with radial pore multiple and several kinds of axial parenchyma arrangements: diffuse, diffuse-in-aggregates with a tendency toward banded, and vasicentric, × 140. FIG. 10.—*Passiflora arborea* Spreng. Tangential section of wood showing biseriate heterocellular vascular rays with long uniseriate wings. Libriform wood fibers have thick walls, × 200.

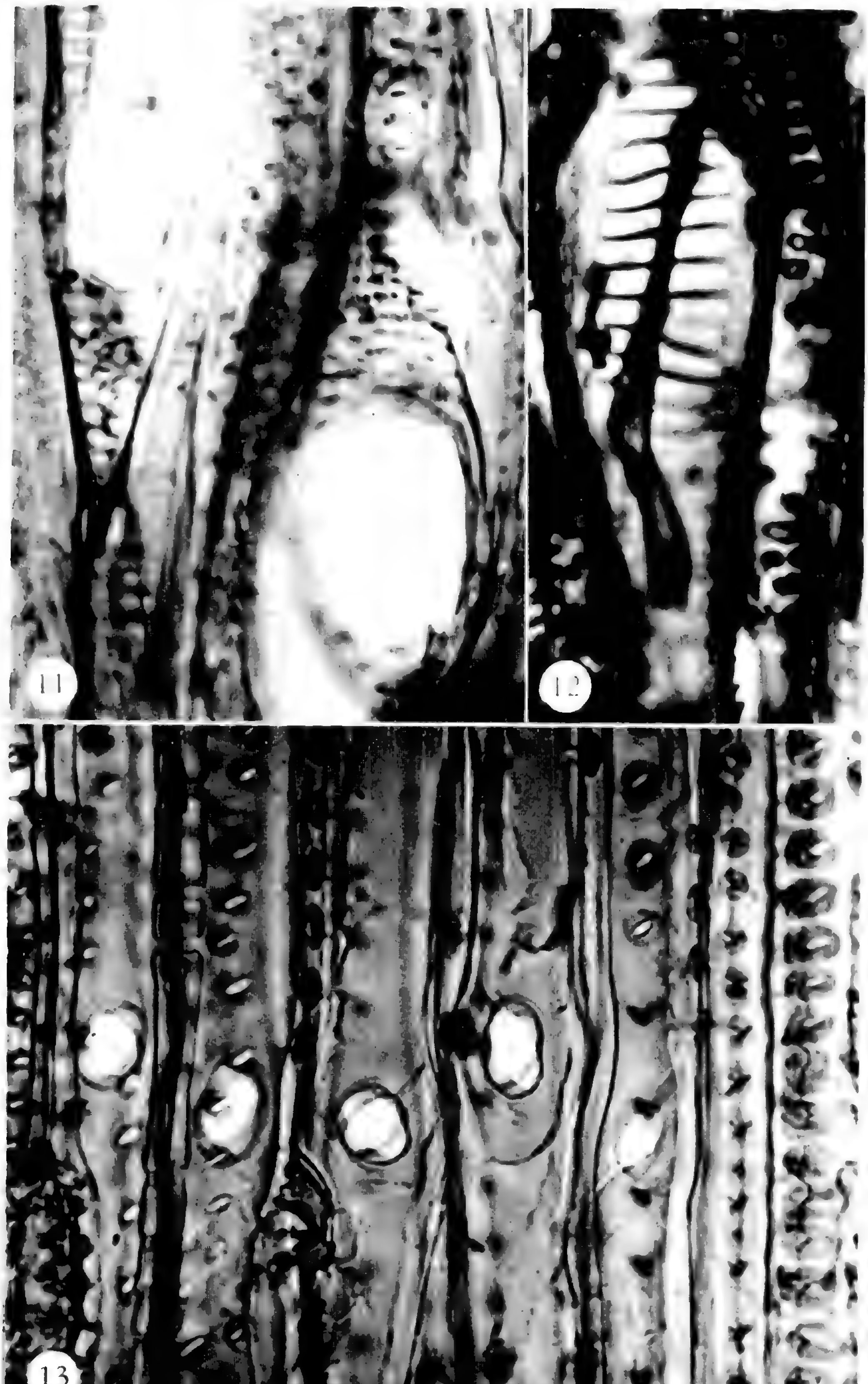
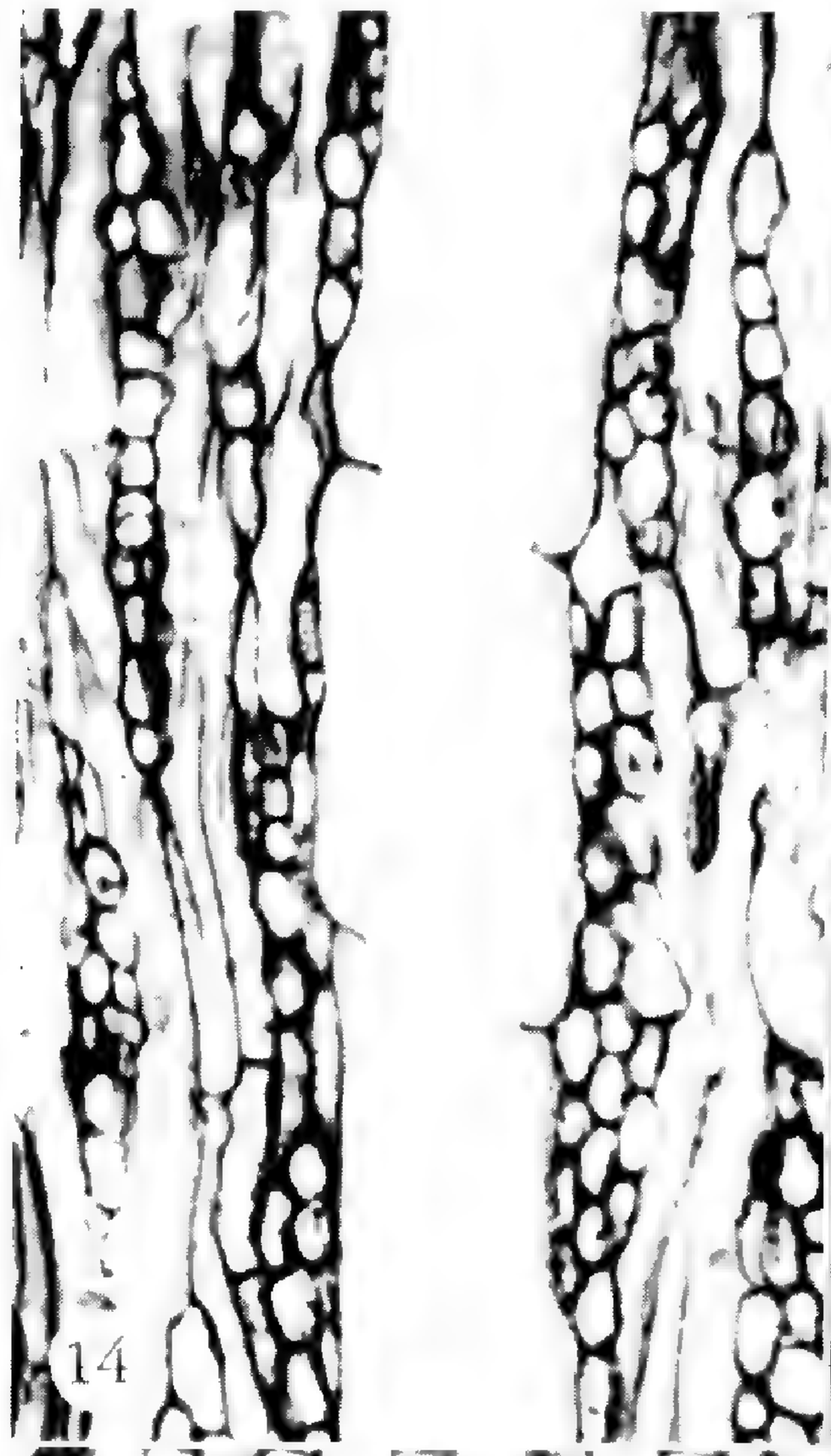


FIG. 11. *Pa* [illegible] ×50. FIG. 12. *Pa* [illegible] Tangential section of xylem showing [illegible] ×50. FIG. 13. *Pa* [illegible] Tangential section of xylem showing [illegible] ×200.



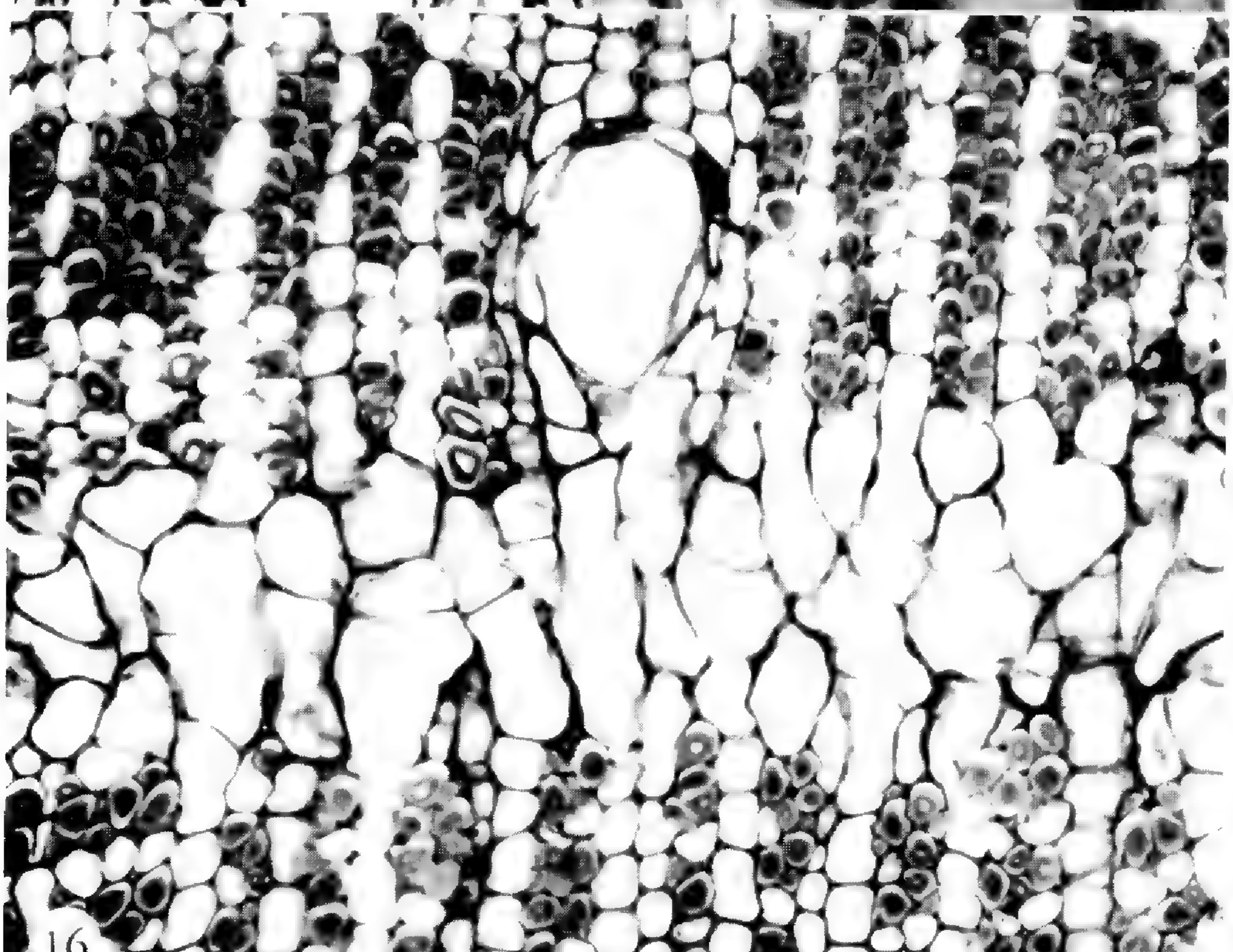


FIG. 14. *Passiflora mollissima* (H. B. K.) Bailey. Tangential section of wood illustrating oblique vessel element end walls, × 180. FIG. 15.—*Passiflora elliptica* Gardn. Radial section of wood showing perforated ray cell, × 900. FIG. 16.—*Passiflora arborea* Spreng. Transverse section of xylem showing a large pith fleck, × 150.

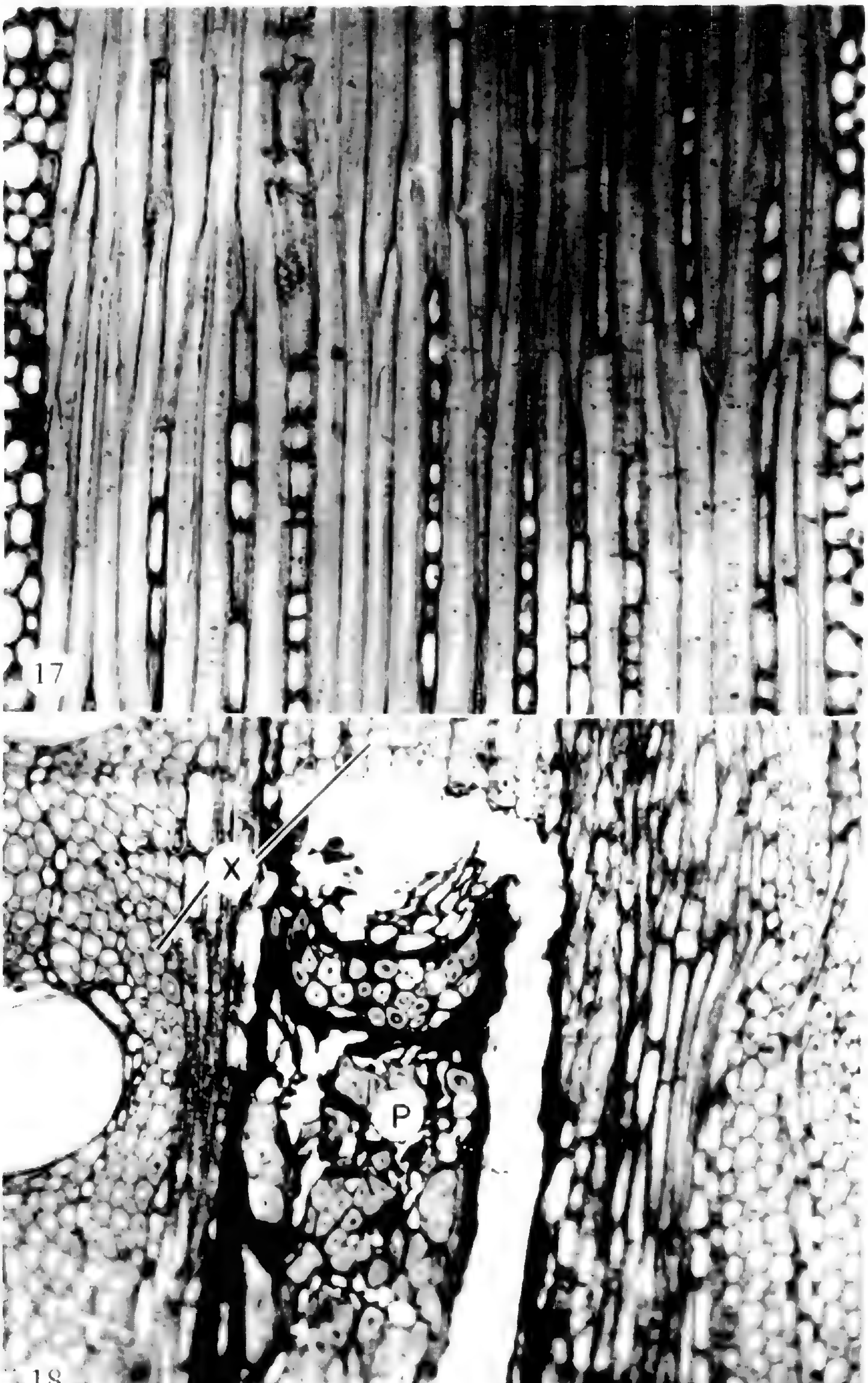
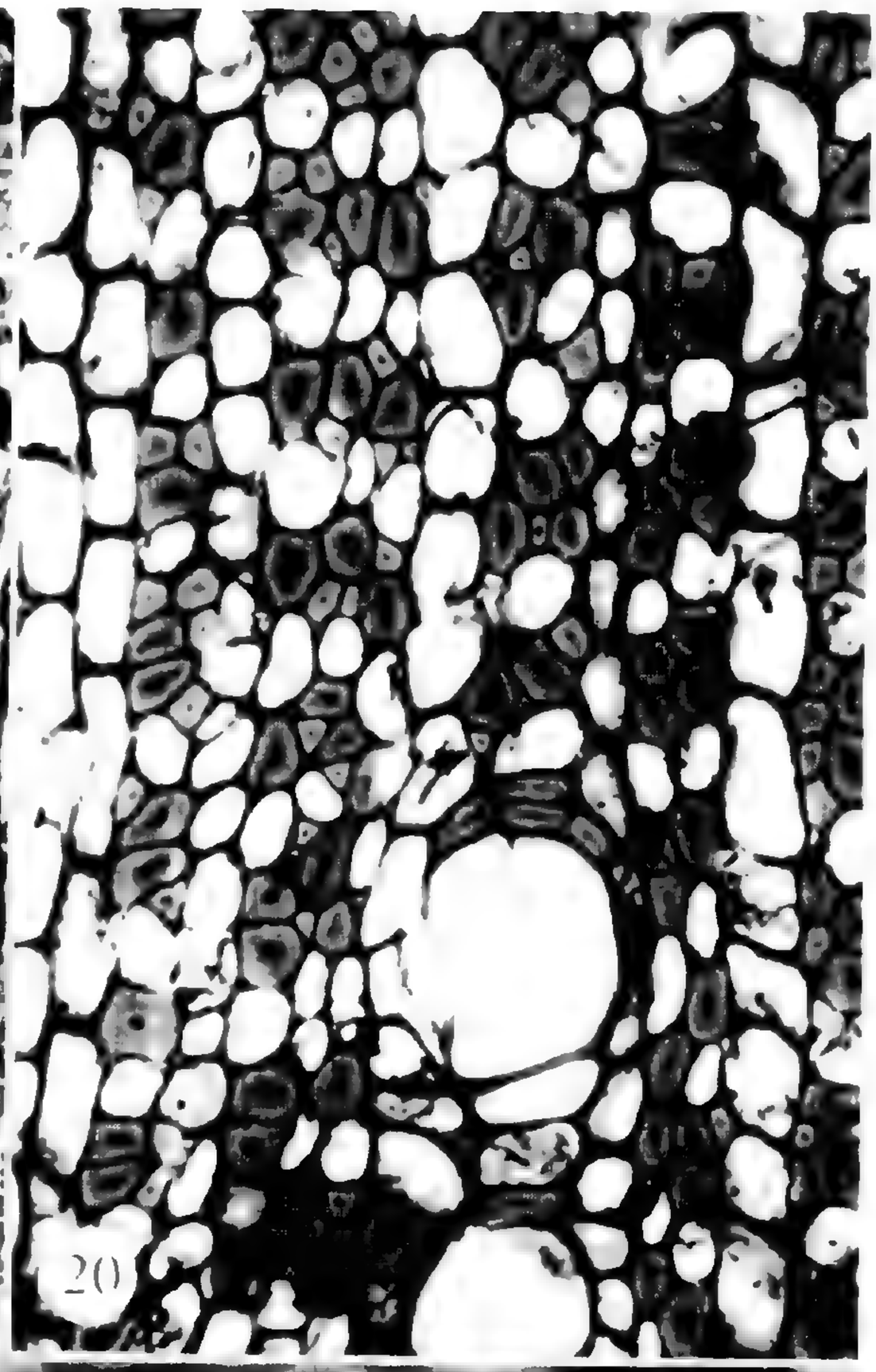


FIG. 17. *Pachyphloia ovalifolia* Cav. Tangential section of two lobes showing storied arrangement of uniseriate rays, and 1 to 4, wide, non-storied multiseriate rays. × 160. FIG. 18. *Pachyphloia ovalifolia* Cav. Transverse section of root stem at base of fan, showing xylem-phloem interface as seen in the interrupted type of anomalous development; X, xylem; P, phloem. 150



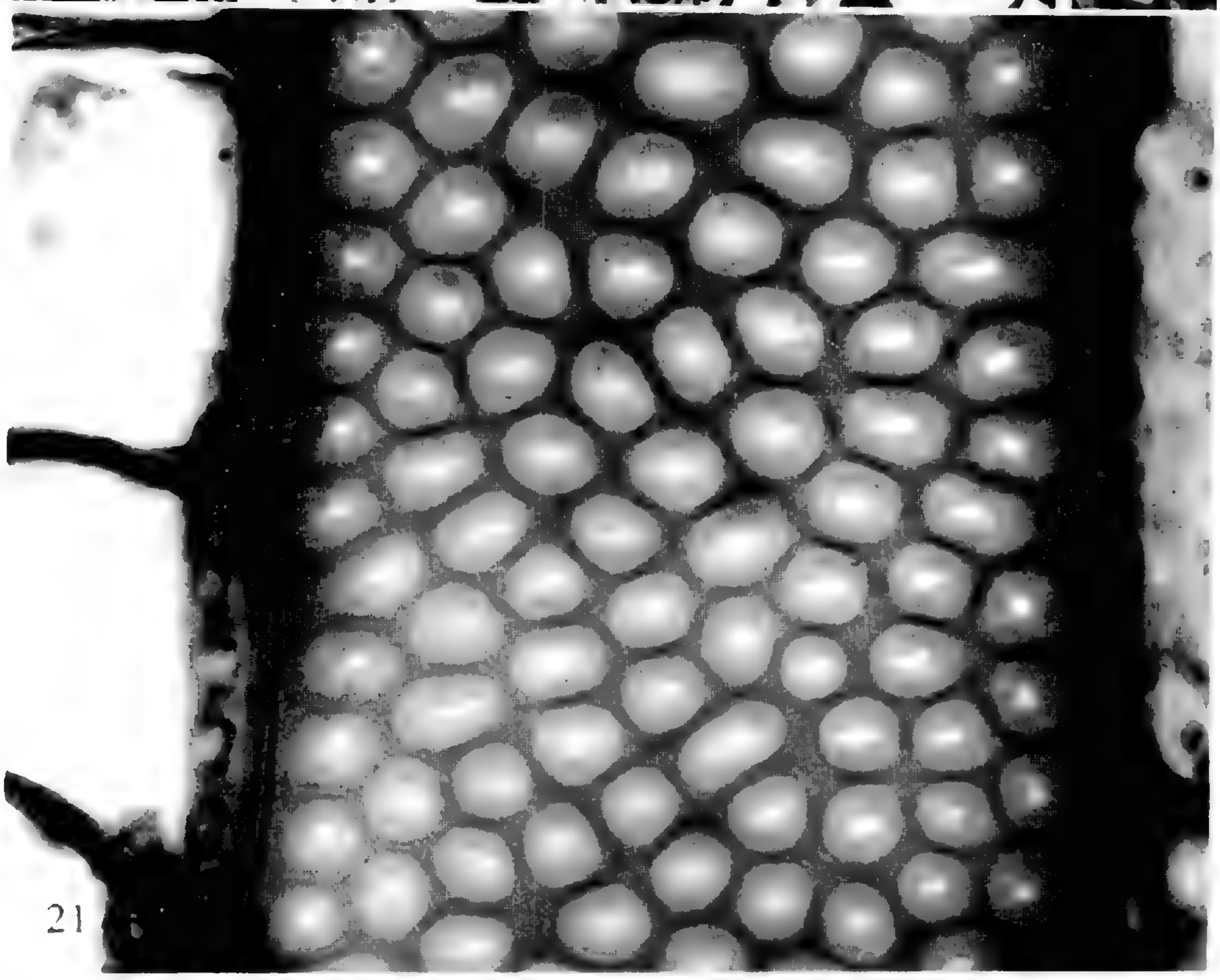


FIG. 19.—*Passiflora coccinea* Aubl. Transverse section of stem along xylem-phloem interface as seen in the interrupted type of anomalous development; x = xylem, p = phloem, × 150. FIG. 20. *Paropsia madagascariensis* (Baill.) H. Perrier. Transverse section of xylem illustrating the occurrence of abundant axial parenchyma in diffuse in aggregates arrangement, × 150. FIG. 21.—*Passiflora arborea* Spreng. Tangential section of wood showing alternate intervascular pitting, × 900.

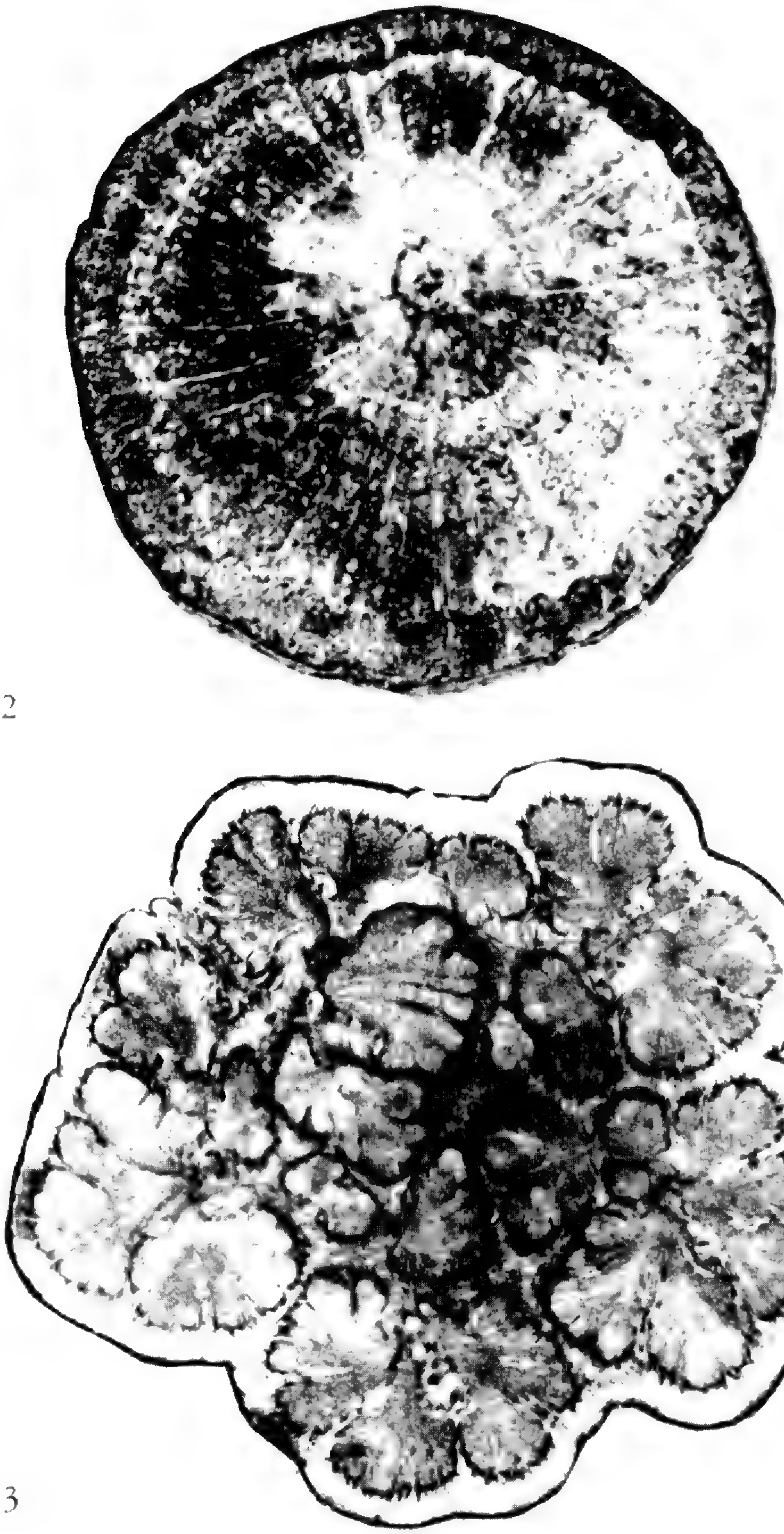


FIG. 22.—*Passiflora fuchsiiflora* Hemsl. Transverse section of stem showing normal type of development, × 2.8. FIG. 23.—*Passiflora multiflora* L. Transverse section of stem illustrating dispersed type of anomalous structure, × 2.

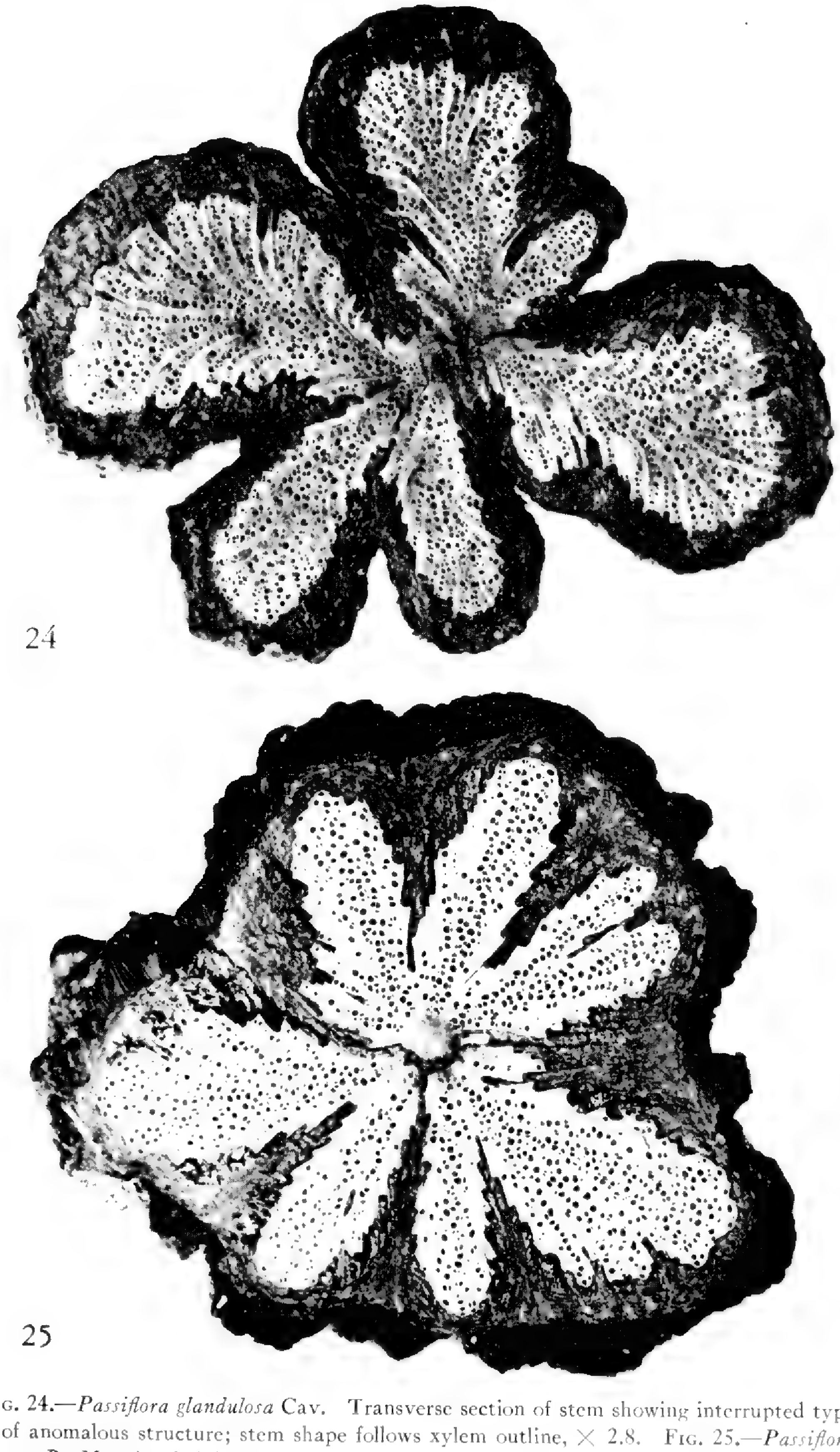
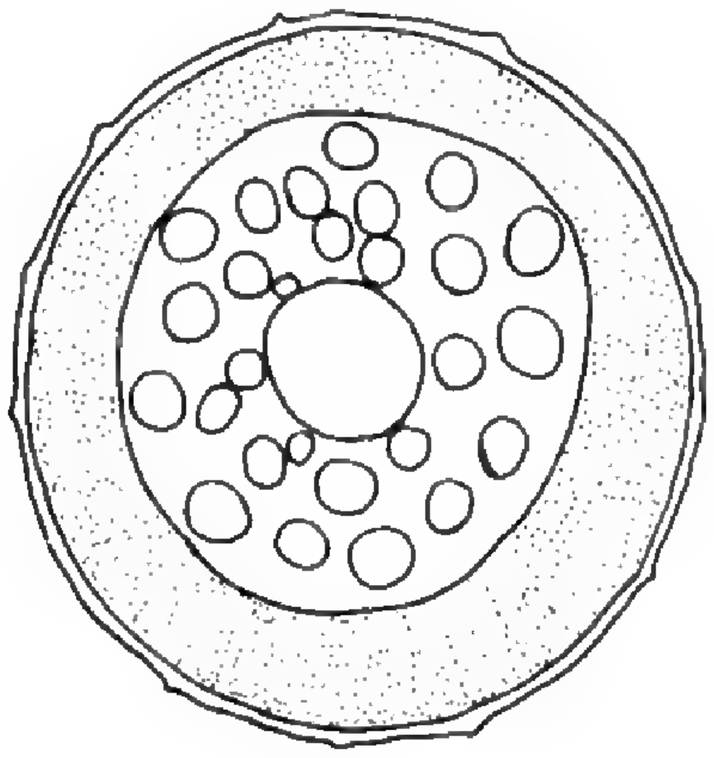
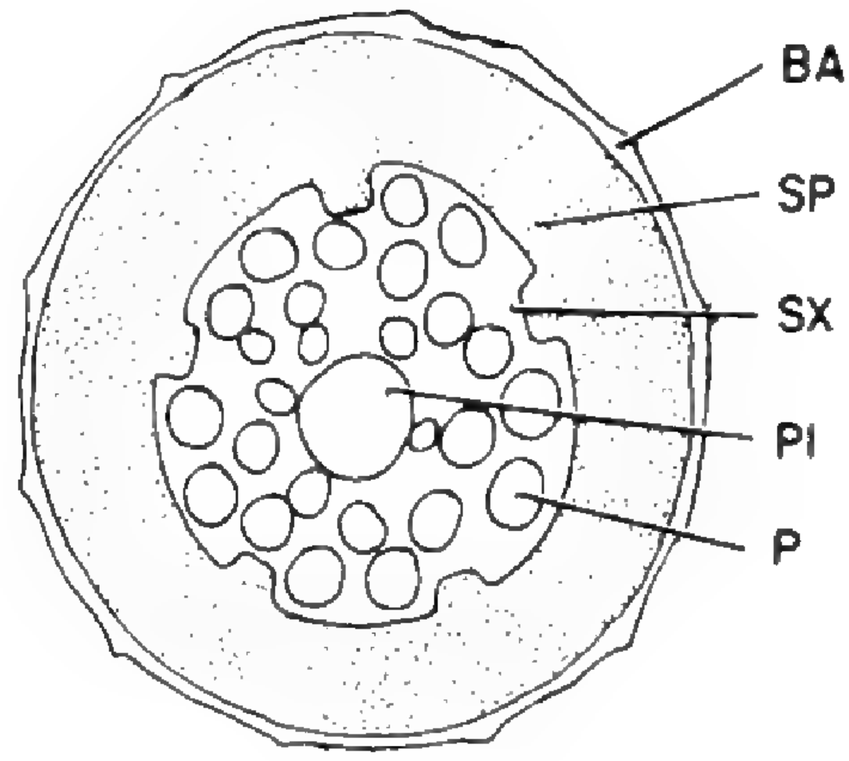
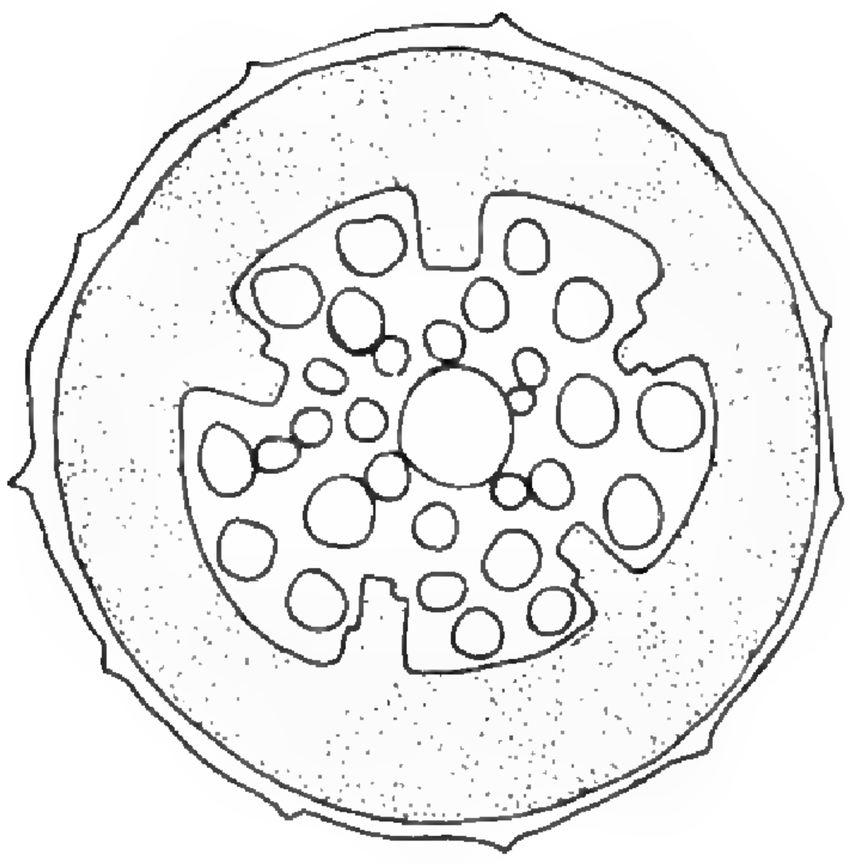
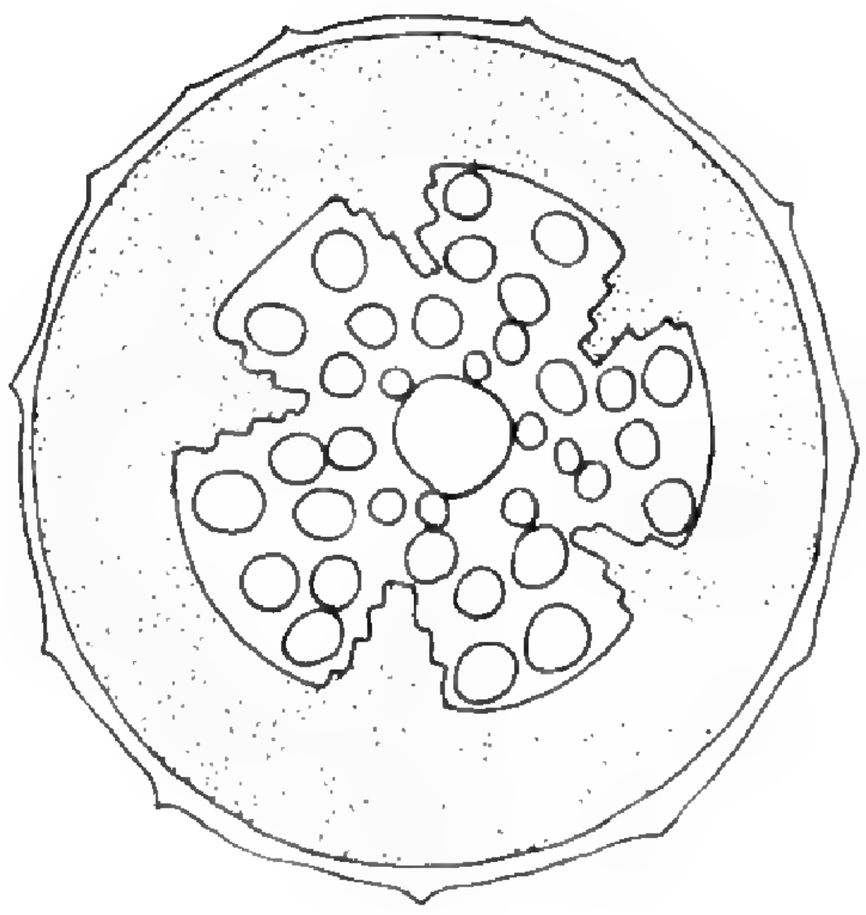


FIG. 24.—*Passiflora glandulosa* Cav. Transverse section of stem showing interrupted type of anomalous structure; stem shape follows xylem outline, × 2.8. FIG. 25.—*Passiflora* sp. *B. Maguire 28327.* Transverse section of stem illustrating interrupted type of anomalous structure; stem outline hardly reflects xylem configuration, × 3.3.









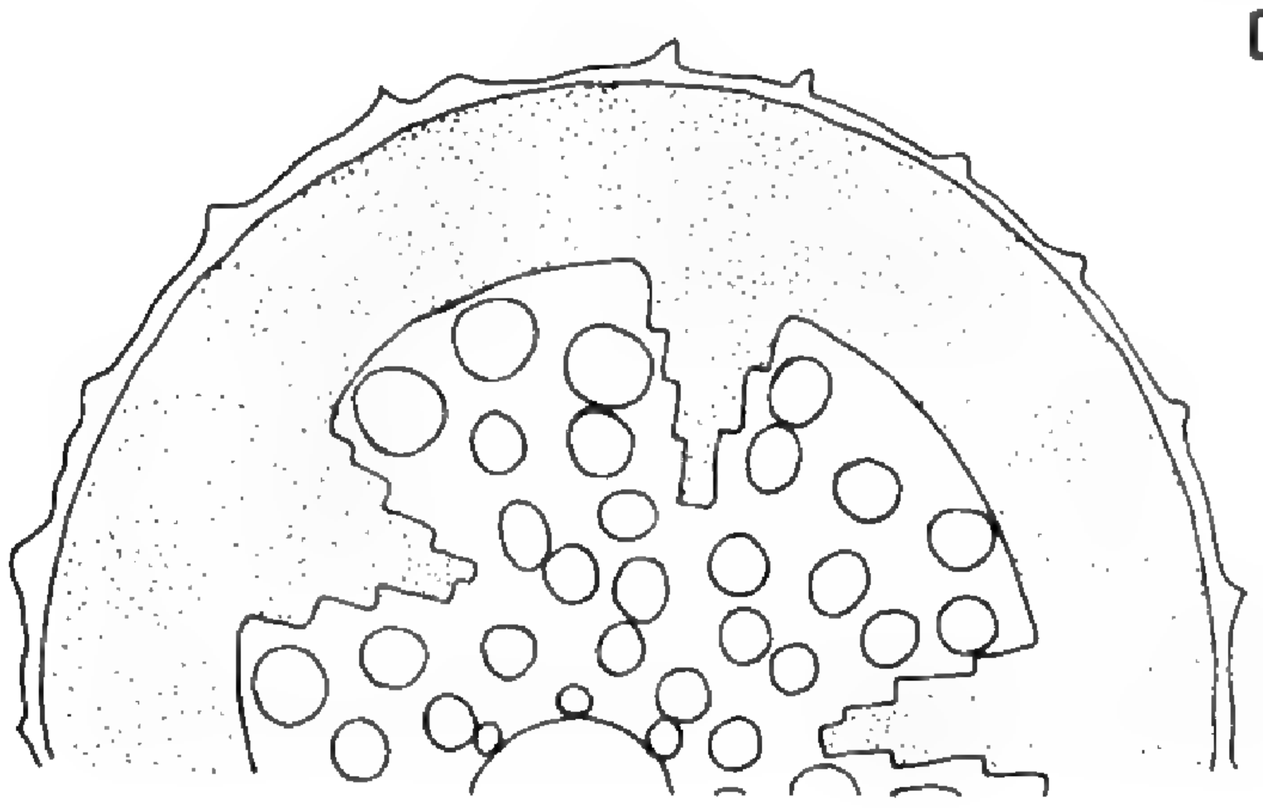


FIG. 26.—*Passiflora glandulosa* Cav. Ontogeny of the stem in serial transverse sections: A, an early internode depicting normal development at this stage; B, a later internode illustrating incipient formation of furrows in the vascular cylinder; C, D, E, phases leading to development of steplike configuration which results from unequal production of secondary xylem and phloem. BA=bark, SP=secondary phloem, SX=secondary xylem, PI=pith, P=pore.

element end wall inclination oblique to transverse; intervascular pitting alternate; imperforate tracheary elements fiber-tracheids, average length 388 μ, range 208 μ–482 μ; fibriform vessel members present; vascular rays mainly uniseriate 1–15 cells high, few multiseriate 2–4 cells wide, few very high multiseriate rays, heterocellular; axial parenchyma diffuse; crystals present in ray cells; uniseriate rays vaguely storied; stem anomalous (interrupted); pith flecks present.

Passiflora quadriglandulosa: Growth rings absent; pores mainly solitary, rounded, average diameter 161 μ, range 73 μ–207 μ; average vessel element length 283 μ, range 203 μ–417 μ; vessel wall thickness 2 μ–5 μ; perforation plates simple; vessel element end wall inclination oblique to transverse; intervascular pitting alternate; imperforate tracheary elements fiber-tracheids, average length 420 μ, range 374 μ–513 μ; fibriform vessel members present; vascular rays uniseriate 1–15 cells high, and multiseriate 2–many cells wide and 2–many cells high, heterocellular; axial parenchyma diffuse; crystals absent; uniseriate rays storied; stem anomalous (interrupted); pith flecks present.

Passiflora securiclata: Growth rings absent; pores 80 percent solitary, 20 percent radial multiples, rounded, average diameter 125 μ, range 101 μ–150 μ; average vessel element length 268 μ, range 217 μ–301 μ; vessel wall thickness 6 μ–7 μ; perforation plates simple; vessel element end wall inclination transverse; intervascular pitting opposite; imperforate tracheary elements fiber-tracheids, average length 461 μ, range 328 μ–424 μ; fibriform vessel members present; vascular rays mainly multiseriate without uniseriate extensions, 2–14 cells wide, 8–16 cells high, few uniseriate 1–8 cells high, mostly 3–6 cells high, heterocellular; ray cells with simple perforations; axial parenchyma diffuse, and with a few narrow bands; crystals present in ray cells; storying absent; stem normal; pith flecks present.

Passiflora vitifolia: Growth rings absent; pores mainly solitary, rounded, average diameter 160 μ, range 104 μ–196 μ; average vessel element length 372 μ, range 214 μ–472 μ; vessel wall thickness 3 μ–5 μ; perforation plates simple; vessel element end wall inclination transverse; intervascular pitting alternate; imperforate tracheary elements fiber-tracheids, average length 455 μ, range 411 μ–549 μ; fibriform vessel members present; vascular rays multiseriate, 2–many cells wide and few uniseriate 1–8 cells high, few very high multiseriate rays, heterocellular; ray cells with simple perforations; axial parenchyma diffuse; few crystals present in ray cells; storying absent; stem anomalous (interrupted); pith flecks present.

Passiflora sp. *Jonker & Daniels 1227:* Growth rings absent; pores 50 percent solitary, 30 percent radial multiples, 20 percent clusters, rounded, average diameter 125 μ, range 94 μ–178 μ; average vessel

element length 344 μ, range 311 μ–433 μ; vessel wall thickness 2 μ–4 μ; perforation plates simple; vessel element end wall inclination transverse; intervascular pitting opposite to alternate; imperforate tracheary elements fiber-tracheids, average length 487 μ, range 431 μ–571 μ; fibriform vessel members present; vascular rays mainly multiseriate 2–4 cells wide, few uniseriate 1–9 cells high, some very high multiseriate rays, homocellular, consisting solely of upright cells; axial parenchyma diffuse with a few narrow bands; crystals absent; uniseriate rays storied; stem apparently anomalous (included phloem); pith flecks present.

Smeathmannia laevigata: Growth rings absent; pores mainly in radial multiples, rounded, average diameter 84 μ, range 56 μ–101 μ; average vessel element length 570 μ, range 466 μ–691 μ; vessel wall thickness 2 μ–3 μ, perforation plates simple; vessel element end wall inclination oblique; intervascular pitting alternate; imperforate tracheary elements fiber-tracheids and libriform wood fibers, average length 472 μ, range 422 μ–801 μ; fibriform vessel members absent; vascular rays mainly uniseriate 1–9 cells high, few biseriate 4–8 cells high, heterocellular; axial parenchyma diffuse; crystals absent; storying absent; stem normal; pith flecks absent.

Smeathmannia pubescens: Growth rings vague; pores mainly in radial multiples, rounded, average diameter 87 μ, range 62 μ–113 μ; average vessel element length 590 μ, range 520 μ–674 μ; vessel wall thickness 2 μ–3 μ; perforation plates simple; vessel element end wall inclination oblique; intervascular pitting alternate; imperforate tracheary elements mostly libriform wood fibers, few fiber-tracheids, average length 431 μ, range 410 μ–792 μ; fibriform vessel members absent; vascular rays mainly multiseriate without uniseriate extensions, 2–3 cells wide, 3–8 cells high, some uniseriate 8–13 cells high, heterocellular; axial parenchyma diffuse, and in narrow bands; crystals present in ray cells; storying absent; stem normal; pith flecks absent; gummy deposits present in ray cells and vessel elements.

Ontogeny of the Stem

Ontogenetic investigations are based on series of transverse sections from the stems of four species of *Passiflora: P. auriculata, P. fuchsiiflora, P. glandulosa,* and *P. multiflora.* Prepared slides of the last species were utilized from the earlier study by Stern and Brizicky.

Passiflora fuchsiiflora: Ontogenetic series in this species illustrate only NORMAL (fig. 22) stem development, even in the very mature portions.

Passiflora glandulosa: Transverse sections of the youngest portions of the stem are quite normal and consist of concentric cylinders of

secondary xylem, vascular cambium, and secondary phloem around a central pith (fig. 26A). The vascular cambium, in these early stages, produces xylem and phloem in the usual fashion. At the fifth or sixth node from the tip of the stem, the vascular cylinder becomes furrowed; four, five, or six such furrows occur around the stem as a result of unequal production of xylem and phloem by the vascular cambium, more phloem than xylem being produced in the furrows (fig. 26B). As the stem ages and expands, tangential fragments of the vascular cambium remain behind to form steps at the margins of the furrows between the xylem and phloem (figs. 26C–E). These fragments of cambium along the margins of the furrows continue to produce secondary xylem and phloem in such a manner that a steplike configuration (fig. 26E) is produced as in some species of *Bignonia* (Schenck 1893). An interface between xylem and phloem as it occurs along the margin of a furrow is illustrated in figures 18 and 19. This stem configuration (figs. 24, 25) is designated the INTERRUPTED type, after Pfeiffer (1926, 1927).

Passiflora multiflora: A detailed ontogenetic study of the stem of this species was made by Stern and Brizicky. Essentially, the xylem cylinder is quite normal when young, as is the case in the other species studied. However, as growth of the stem parenchyma cells proceeds, the tracheary elements of xylem and phloem become separated into irregular masses by the dilation of the thin-walled pith and cortical cells, and cells of axial and radial xylem parenchyma. Each tracheary mass appears to be associated with a fragment of vascular cambium, and as a result of this irregularity the production of xylem and phloem proceeds in different directions and at different rates. The resultant anomalous developmental pattern (fig. 23) resembles that which occurs in some species of *Bauhinia* (Schenck 1893). The DISPERSED nature of xylem and phloem strands results from the rupturing of the vascular cambium by parenchyma cells, and the subsequent action of the disoriented bits of vascular cambium (Pfeiffer 1926, 1927; Stern and Brizicky 1958).

Passiflora auriculata: This species is generally normal in its ontogeny. In the mature portions of the stem, however, isolated phloem strands are formed in the secondary xylem which appear as patches on the transverse section. The production of INCLUDED phloem is quite erratic and phloem islands often appear radially oriented within the xylem mass. Phloem islands occur when the cambium, sporadically and briefly, produces phloem centripetally, followed by longer periods of normal xylem production. This type of anomalous development corresponds to the "foraminate type" of Pfeiffer (1926, 1927).

Discussion

Any interpretation of xylem anatomy and taxonomy in Passifloraceae must take into consideration the interrelationships between microscopic structure and plant form. That anatomical structure may be especially modified in response to habit has been clearly pointed out by Bailey (1957) and described in certain tribes of Compositae by Carlquist (1959, 1960). Habit-related anatomical modifications may be superimposed upon specializations related to phylogeny, and the separation of these two facets of structural change is not always clear cut.

The Passifloraceae under study are either lianas or trees. Lianas are specialized plants among dicotyledons and have developed certain easily seen external modifications in response to this habit, such as tendrils and recurved hooks. The stem is attenuated; that is, narrow in transverse section in relation to the extreme length of the plant. In their study of the water-conducting system in climbers, Westermaier and Ambronn (1881) asserted that this feature represented an effective impediment to the flow of water in the stem. They argued that the relatively small cross section of stem available for the ontogenetic deposition of conducting elements and the great length of the conducting region were related to the anatomical peculiarities often evident in lianous stems. To counteract these morphological obstacles, anatomical development has been modified accordingly. Thus, in the case of vessels, a serious hindrance to rapid flow is the adhesion of water to the vessel walls. Broadening of vessels and elimination of scalariform perforation plates are two anatomical modifications which would tend to offset this limitation. A groundmass of thin-walled, conductive tracheids, as opposed to thick-walled, supportive libriform wood fibers, would also act to increase the area available for water transport.

Table 2 contains data from which a number of interesting correlations between anatomical structure and habit may be drawn. Without exception, all trees have libriform wood fibers as well as fiber-tracheids; none of the lianous species possesses libriform wood fibers, and the groundmass of the xylem consists of fiber-tracheids and tracheids. Fibriform vessel members occur in the lianous species of *Passiflora* and in *Paropsia schliebenii*, a tree. Noteworthy in this instance, is that these peculiarly modified cells have not been seen in the rare *Passiflora maguirei*, a vine, nor do they occur in the lianous species of *Crossostemma*, *Dilkea*, or *Mitostemma* which were available to us. All lianous species are characterized by predominantly solitary pores; only among certain tree species are the pores mostly in groups. An exception is *Passiflora elliptica*. The mean diameter of pores in

TABLE 2—*Salient anatomical characteristics in the stems of Passifloraceae*

[+ = present; − = absent; ± = more or less]

Species	*Tree*	*Liana*	*Stem anomalous*	*Fiber-tracheids, or fiber-tracheids and tracheids*	*Libriform wood fibers, or libriform wood fibers and fiber-tracheids*	*Fibriform vessel members*	*Vessels*							*Storied structure*	*Perforated ray cells*	*Opposite intervascular pitting*
							Pores				*Average vessel element length in μ*	*End wall angle*				
							Average diameter in μ	*Distribution*				*Predominantly transverse*	*Transverse and oblique*	*Predominantly oblique*		
								Predominantly solitary	*Solitary and grouped*	*Predominantly grouped*						
Crossostemma laurifolium		+	+	+		−	198	+			424	+			±	−	+
Dilkea johannesii		+	−	+		−	205	+			378	+			±	−	−
Mitostemma glaziovii		+	−	+		−	112	+			416	+			−	−	−
Paropsia adenostegia	+		−		+	−	50	+			450			+	−	−	−
Paropsia madagascariensis	+		−		+	−	85			+	468		+		−	−	−
Paropsia schliebenii	+		−		+	+	45			+	590		+		±	−	−
Paropsia vareciformis	+		−		+	−	70			+	480	+			±	−	−
Passiflora arborea	+		−		+	−	130		+		343		+		−	−	−
Passiflora auriculata		+	+	+		+	210	+			362	+			+	−	+
Passiflora coccinea		+	+	+		+	210	+			385		+		+	−	−
Passiflora edulis		+	+	+		+	131	+			185	+			+	−	+
Passiflora elliptica		+	−	+		+	117			+	316		+		±	−	+
Passiflora fuchsiiflora		+	−	+		+	135	+			396		+		±	−	+
Passiflora glandulosa		+	+	+		+	200	+			341		+		+	−	−
Passiflora laurifolia		+	−	+		+	124	+			318		+		±	−	+
Passiflora maguirei		+	−		+	−	75	+			211		+		±	−	−
Passiflora mollissima		+	−	+		+	111	+			368		+		±	+	+
Passiflora multiflora		+	+	+		+	128	+			345	+			+	−	−
Passiflora nitida		+	+	+		+	138	+			234		+		±	−	−
Passiflora quadriglandulosa		+	+	+		+	161	+			283		+		+	−	−
Passiflora securiclata		+	−	+		+	125	+			268	+			−	+	+
Passiflora vitifolia		+	+	+		+	160	+			372	+			−	+	−
Passiflora sp. (*Jonker Daniels 1227*)		+	+	+		+	125		+		344	+			+	−	+
Smeathmannia laevigata	+		−		+	−	84			+	570			+	−	−	−
Smeathmannia pubescens	+		−		+	−	87			+	590			+	−	−	−

the lianous species of Passifloraceae is 148 μ, species averages ranging from 75 μ–210 μ. On the other hand, pores average 78 μ in diameter in the trees, the species averages ranging from 45 μ–130 μ. Two points should be raised in this connection: *Passiflora arborea*, an arboreal species, has an average pore diameter which exceeds that in some of the lianous species, and *Passiflora maguirei*, a lianous species, has an average pore diameter less than that in some of the arboreal species. Vessel element lengths also appear to be correlated with habit; that is, average vessel element length in tree species is longer (498 μ; range 343 μ–590 μ) than in lianous species (330 μ; range 185 μ–424 μ). Strictly transverse vessel element end walls occur only in

certain lianous species, and strictly oblique vessel element end walls are confined to certain arboreal species. Most Passifloraceae exhibit both types of end walls. The only case of scalariform perforation plates is found in *Paropsia adenostegia*, a tree. Two further correlations may be noted: Opposite intervascular pitting and anomalous stem structure have been seen only in lianous species.

Overlooking the few obvious exceptions mentioned above, some important generalizations can be stated concerning stem anatomy in Passifloraceae. Vines have shorter vessel elements and broader vessels which are solitary in distribution. Furthermore, they possess fiber-tracheids and tracheids, along with fibriform vessel members. Trees, on the other hand, have longer vessel elements and narrower vessels which are inclined to be grouped in distribution; fibriform vessel members are absent. These generalized correlations of anatomical structure with habit can be interpreted reasonably only on a physiological, rather than on a phylogenetic, basis. Considered in conjunction with previous statements on the water-conducting system in lianas, and the special anatomical problems associated with these attenuated stems, it is easy to see that the xylem anatomy of these vines is particularly modified to increase the flow of water. Besides the evident facilitation of this process by the broad vessels composed of short elements, it is altogether likely that the fiber-tracheids, tracheids, and fibriform vessel members play an active part in support of this function. These anatomical modifications, coupled with others mentioned above, are doubtlessly related to water conduction in the lianous species. It is in the wood structure of the trees, therefore, that a search must be made for those anatomical modifications related to phylogenetic specialization in Passifloraceae.

The most reliable indicators of evolutionary trends in the xylem of dicotyledons are the development and subsequent specialization of vessels (Bailey 1957). Long, attenuated, angular vessel elements with many-barred scalariform perforation plates and scalariform intervascular pitting most closely resemble tracheids, and on this basis are regarded as most primitive. Short, truncated, rounded vessel elements with simple perforation plates and alternate intervascular pitting are least like tracheids and are considered most advanced. Correlations between trends of vessel specialization and concurrent modification of associated tissues have been employed in reaching conclusions relative to the phylogenetic development of imperforate tracheary elements, and radial and axial parenchyma, for example.

The totality of evidence from the xylem of arborescent Passifloraceae points to attainment of a moderate stage of phylogenetic specialization by these plants. Vessel elements average about

500 μ in length, less than the 649 μ average for 600 dicotyledons.[2] Vessel diameters average 80 μ, somewhat less than the 94 μ average for 1500 dicotyledons. Imperforate tracheary elements are considerably shorter on the average (582 μ) than the 1317 μ average for 534 dicotyledons. Vessels are rounded in transverse section and pores are either predominantly grouped, or comprise grouped and solitary distributions. Intervascular pitting is alternate, and perforations are simple in all species; however, scalariform perforations also occur in *Paropsia adenostegia* and perhaps in other species. Imperforate tracheary elements are libriform wood fibers and fiber-tracheids; some species possess libriform wood fibers exclusively, but none exhibits solely fiber-tracheids. Vascular rays are largely heterocellular, although in *Paropsia schliebenii* and *P. vareciformis* homocellular rays have been recorded. Axial parenchyma is generally diffuse in nature, but the vasicentric configuration occurs in *Passiflora arborea* in conjunction with the diffuse and diffuse-in-aggregates types. Storied structure is absent in most species. Interestingly, the two species which show homocellular vascular rays also exhibit a tendency for storying in the rays. Storying and homocellular rays are often considered as advanced characteristics. Among the arboreal Passifloraceae on hand for this study, there does not appear to be any trend in xylem specialization to indicate an evolutionary series of any kind. Because Metcalfe and Chalk mention the occurrence of scalariform intervascular pitting and scalariform perforation plates in species and genera of which we have no representation (e.g., *Androsiphonia* and *Barteria*), it is likely that with a broader range of material trends of specialization in the xylem of the arboreal Passifloraceae would become evident.

Three types of anomalous stem development have been observed from ontogenetic studies. Material for these studies was available only in the genus *Passiflora*, although *Crossostemma laurifolium* also exhibits an anomalous stem. The anomalous growth in *Passiflora multiflora* is quite distinct, and is caused by the dilation of the parenchymatous elements of the xylem which disrupts the cambium, subsequently to form irregular masses of tracheary tissue. Thin-walled xylem parenchyma is necessary for the accomplishment of such a process. Although this type of anomalous development also occurs in *Bauhinia*—Leguminosae and in other plants it would be ludicrous to assume any genetic relationship here. Bailey (1957) has cautioned, that because ". . . similarities due to parallel evolution are surprisingly common in the xylem of dicotyledons" they cannot be utilized in positive assertions of relationship or phylogenetic

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[2] Data on general anatomical averages are from appendices in Metcalfe and Chalk (1950).

derivation without corroborative evidence from other parts of the plant.

The unique stem in *Passiflora multiflora* appears to lend credence to Killip's original suggestion that the species be segregated into a genus on the basis of its sessile ovary. Along these lines it might be well to point out here the occurrence of anomalous stems and storied rays among several subgenera of *Passiflora*. These two features, thus, probably have little taxonomic significance on the species level.

Stern and Brizicky noted that anomalous stem structure, somewhat similar to that in *Passiflora multiflora*, also occurs in *Passiflora coccinea* (subgenus *Distephana*). Present studies indicate, however, that the anomalous stem growth in *Passiflora coccinea* results from tangentially unequal production of secondary xylem and phloem by the vascular cambium (interrupted type) and not from disrupted and displaced layers of cambium (dispersed type).

Earlier investigators (Masters 1871, Schenck 1893, Solereder 1908, Killip 1938, Metcalfe and Chalk 1950, Boureau 1957) may have overlooked the anomalous stem condition in Passifloraceae because it ordinarily becomes apparent only in the older portions of the stem not normally included in herbarium specimens. However, in *Passiflora glandulosa*, the unequal development of xylem and phloem proceeds very early in ontogeny. The time of attainment of the mature ontogenetic pattern is not consistent among the species studied, and it may be strictly genetic, or influenced by edaphic or other environmental stimuli.

From the above descriptions of the ontogeny of the stem in Passifloraceae, it appears that the most specialized and highly modified is the dispersed type of configuration exemplified by *Passiflora multiflora*. It might be of interest to speculate on the phylogenetic development of this type of stem in Passifloraceae, and upon its relationship, if any, to the other types described here. Reference to figures of this paper, and to the developmental sequences depicted in the Stern and Brizicky paper, points to the possibility that the dispersed type of vascular cylinder may have developed phylogenetically from the interrupted type by continued distention of cells in the parenchymatous groundmass to rupture the vascular cambium completely. This phenomenon would have to be coupled with, and preceded by, unequal production of secondary xylem and phloem. The ontogeny of the stem of *P. multiflora* shows stages of development representative of the interrupted type of configuration as seen in *P. glandulosa*. On the other hand, the production of included phloem in Passifloraceae might be viewed as another offshoot of the unequal production of secondary xylem and phloem. In this case, the unequal production

never became associated with rupturing of the vascular cylinder brought on by distention of cells in the parenchymatous groundmass, and the basic integrity of the vascular cylinder was continually maintained.

In the course of this investigation we observed cells that Woodworth (1935) termed "fibriform vessel members." Originally (1934), he assigned the name "perforated fiber-tracheids" to these same structures, which perhaps best describes these elements. Woodworth explained later, however, that "for purposes of definition, this descriptive phrase is unfortunate," because in effect it means, perforated, imperforate cells. Basically, these are elongate elements, similar in most respects to fiber-tracheids, except for the presence of simple perforations. From the structural standpoint, fibriform vessel members resemble fiber-tracheids on the one hand, and vessel elements on the other. They incorporate within the same cell the greater length and fusiform shape of the fiber-tracheid with the perforation plates of vessel elements.

Such a combination of features calls for a reconsideration of the basic distinction between the two cell types; that is, imperforate element *vs.* vessel (perforate) element. According to the *International glossary of terms used in wood anatomy* (Committee on Nomenclature 1957), a vessel is an axial series of cells where the cells have coalesced to form an articulated, tubelike structure of indeterminate length. This designation implies that a vessel may consist of but two cells interconnected by perforations; by definition, therefore, two axially aligned fibriform vessel members must be considered a vessel.

Even though the occurrence of the fibriform vessel member is greatly restricted taxonomically, and use of the term is correspondingly limited on this account, the name is inadequately descriptive, and more importantly, it has misleading phylogenetic implications. Woodworth was aware of these factors, and considered them in justifying the use of his term. In every respect these cells resemble imperforate tracheary elements except for the presence of perforations; they bear little resemblance to normal vessel elements in the same wood. Furthermore, the perforation is ordinarily intercalated between the ends of the cells, and the terminations of these cells have little if any similarity to the ligulate ends of normal vessel elements where ligulae occur. The perforation itself is aberrant, usually small in size, poorly formed, and unlike those in normal vessel elements. These cells are twice as long as the fusiform cambial initials from which they have been derived, and differ strongly from normal vessel elements in this way. It is extremely dubious that these cells are allied in any way, ontogenetically or phylogenetically, with true vessel elements. Therefore, to call these cells vessel members of any kind

would be to relate them, even if in name only, with normal vessel elements upon whose phylogenetic modification rests our entire scheme of evolution in the xylem. Because of these factors, we strongly urge the disuse of fibriform vessel member and the reassumption of Woodworth's original term—perforated fiber-tracheid—to describe these cells despite the obvious ambiguity, viz, a tracheid, by definition, is an imperforate cell.

Although no extensive series of interconnected cells of this type was seen in the species studied, there are interconnections involving two, occasionally three, or even five such cells. Axial continuity between fibriform vessel members and fiber-tracheids also occurs, although no continuity between fibriform vessel members and true vessel elements was noted. That there is actual conduction of fluid between contiguous cells of fibriform vessel members and between fibriform vessel members, fiber-tracheids, and tracheids, is probable in view of the peculiar water transport problems of lianas. Woodworth, on the other hand, remarked that it seems unlikely that the fibriform vessel members contribute significantly to water movement in such plants. Regardless, it does seem entirely reasonable to assume that lianous plants require additional anatomical modifications, such as perforations in fiber-tracheids, to ensure a more efficient water conducting system even if the contribution of these modifications to total water transport is comparatively small. Woodworth examined the xylem of other lianas for fibriform vessel members and located them only in some species of Celastraceae. Notwithstanding the apparent advantage to water conduction in lianas of anatomical modification which would tend to facilitate this phenomenon, it is obvious that the genetic potential for such modification must exist as a preliminary requisite.

The perforated ray cell, which occurs in some species of Passifloraceae, has also been observed by Chalk and Chattaway (1933) in 73 species of 16 unrelated plant families. Different specimens of the same species vary considerably in the number of these cells present. Perforated ray cells are produced when axially oriented vessels bend tangentially to pass through one or more cells of a ray. Perforations in the ray cells usually correspond in kind to the normal perforations in associated vessel elements. Chalk and Chattaway have suggested that from the position of the rays, these cells are developed from ray initials instead of fusiform initials. Since perforated ray cells have such a wide distribution, and are so variable in occurrence even within species, their taxonomic significance is limited.

Pith flecks occur commonly in the species of *Passiflora;* that is, more regularly than if the presence were merely in response to a chance trauma. Although the occurrence of pith flecks is commonly

attributed to outside agents, such as the larvae of cambium miners, their consistent occurrence within the genus *Passiflora* may have minor taxonomic significance. *Passiflora* bark may be especially attractive to certain organisms which seek it out in preference to other food sources. The mutualistic relationship between ant species and myrmecophytes is an example of this kind.

Paropsia, considered previously in this study, has been variously placed in Flacourtiaceae and Passifloraceae. The wood anatomy of *Paropsia* shows considerable similarity to some genera of Passifloraceae, especially *Smeathmannia*, a genus comprising mostly shrubs and trees. Pores mainly in radial multiples, rounded; perforation plates simple in some species; vessel element end wall inclination oblique; alternate intervascular pitting; libriform wood fibers; the occurrence of abundant axial parenchyma; and fibriform vessel members, indicate affinity of *Paropsia* with Passifloraceae. The occurrence of axial parenchyma in *Paropsia* is significant, for this tissue is generally lacking in woods of the Flacourtiaceae (Record and Hess 1943; Tupper 1934). Pollen grain analysis provides further substantiation for aligning *Paropsia* with Passifloraceae. Erdtman (1952) has shown that pollen of both *Passiflora maculifoli* and *Paropsia brazzeana* has a reticulate sexine and measurements of the subprolate grains are 52 μ × 44 μ and 53 μ × 41 μ, respectively. He further suggests that the tribe *Paropsieae* of Flacourtiaceae should, at least in part, be referred to Passifloraceae. Convincing resolution of this problem will depend upon further studies in other botanical disciplines.

Summary

1. Growth rings are absent or inconspicuously developed; rounded pores are mainly solitary and in radial multiples; simple perforation plates and alternate intervascular pitting occur in all species; vessel element end walls vary from oblique to transverse. Imperforate tracheary elements are tracheids, fiber-tracheids, and libriform wood fibers; fibriform vessel members occur in some species. Perforated ray cells are found in a few species. Vascular rays are both heterocellular and homocellular, uniseriate and multiseriate; uniseriate rays are commonly storied. Axial parenchyma is diverse in form and includes a range of types in both apotracheal and paratracheal series.

2. Certain anatomical modifications are correlated with plant form; lianas have shorter vessel elements and broader, solitary vessels; fibriform vessel members are present. Trees show longer vessel elements and narrower, grouped vessels; fibriform vessel members are generally absent. The anatomical modifications in the xylem

of lianas are related to physiology and habit rather than to phylogenetic position.

3. Xylem anatomy of tree species indicates that Passifloraceae is only moderately advanced phylogenetically.

4. Anomalous stem development occurs in *Crossostemma* and *Passiflora*. Ontogenetic series show four types of mature stem configurations in the family: (1) normal type; (2) included phloem type; (3) interrupted type; and (4) dispersed type. It is postulated that the dispersed type of configuration is the most highly modified anomalous stem form in Passifloraceae. It is doubtful that the anomalous stem condition here constitutes a valid taxonomic feature in assuming genetic relationships between Passifloraceae and other families, or that its occurrence provides a basis for taxonomic arrangement within the family.

5. The presence of abundant axial parenchyma and of fibriform vessel members in *Paropsia schliebenii* supports the position that *Paropsia* belongs to Passifloraceae rather than Flacourtiaceae.

6. The substitution of "perforated fiber-tracheid" for "fibriform vessel member" is recommended to avoid possible phylogenetic misconceptions related to the use of the word vessel in this descriptive sense.

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TAXONOMIC STUDY OF SUBGENUS PODOSEMUM AND SECTION EPICAMPES OF MUHLENBERGIA (GRAMINEAE)

By THOMAS R. SODERSTROM

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TAXONOMIC STUDY OF SUBGENUS PODOSEMUM AND SECTION EPICAMPES OF MUHLENBERGIA (GRAMINEAE)

By THOMAS R. SODERSTROM

Introduction

Within the genus *Muhlenbergia* (Gramineae) is a group of tall, rather robust perennials that some botanists have treated as a distinct genus, *Epicampes*. Since Presl (1830) proposed *Epicampes*, many species have been added. All are found in the Western Hemisphere, the majority occurring in northern and central Mexico, the center of distribution.

The characters originally employed to delimit *Epicampes* have been interpreted by botanists in different ways. Some have placed considerable emphasis on the dorsal position of the awn of the lemma, while others have regarded the relatively long glumes of the spikelet as particularly characteristic. Another feature of value is the compressed-keeled nature of the basal sheaths. No one character has been found to distinguish all species of *Epicampes* from all other genera. Authors who have described species in the group have had different concepts of the genus, to the extent that *Epicampes* has never been clearly circumscribed. Unfortunately, no recent author has listed the species considered to comprise the genus *Epicampes*, and not only is the generic status and affinities of the group a problem, there is also no general agreement regarding the number of species.

Traditionally, the classification of grasses has been based on characters of gross morphology, with special reference to the structure of the spikelet. In such a classification *Epicampes* has been treated as a member of the tribe Agrostideae, which includes grasses with single-flowered spikelets, with close affinities to such genera as *Agrostis* and *Cinna*.

Starting before the turn of the century, but more particularly within the last decade, studies of features other than gross morphology have shed much light on the true relationships within the Gramineae. These studies have included investigation of the structure of the grass embryo, lodicules, chromosomes, and the anatomy of the leaf and epidermis. The results of these investigations are correlated remark-

ably and demonstrate that in many cases the characters of the spikelet and other features of gross morphology are not reliable indexes to the natural relationships of grasses. These studies for the most part have dealt with representative species of genera, in an attempt to find their natural affinities within the grass family. Relatively little effort has been made to utilize these studies at the infrageneric level to clarify relationships among the species within a single genus.

The first phase of the present study was to determine the relationship of the Epicampes group at the genus level, and studies of the embryo, lodicules, and leaf anatomy and epidermis were useful in this regard. The results of these investigations provide strong evidence that *Epicampes* is not related to such genera as *Agrostis* and *Cinna* of the Agrostideae but rather to grasses of the "chloridoid" alliance, which includes many grasses traditionally placed within the tribe Chlorideae.

The second phase was a taxonomic survey of the species belonging to the Epicampes group. Field studies were made in Mexico in 1959 and 1960 and herbarium specimens examined included the majority of type specimens or fragments of types of the species involved.

In addition to the large series of specimens studied at Yale University (YU) and the U.S. National Herbarium (US), collections were borrowed from the following herbaria: University of Arizona (ARIZ); California Academy of Sciences (CAS); Escuela Nacional de Agricultura, Chapingo, Estado de México (CHAP); Stanford University (DS); Field Museum of Natural History (F); Gray Herbarium of Harvard University (GH); University of Illinois (ILL); Instituto Politécnico Nacional, México, D.F. (IPN); Texas Research Foundation (LL); Universidad Nacional de Mexico (MEXU); University of Michigan (MICH); Missouri Botanical Garden (MO); New York Botanical Garden (NY); Pomona College (POM); Naturhistoriska Riksmuseum, Stockholm (S); Southern Methodist University (SMU); A.&M. College of Texas (TAES); University of Texas (TEX); University of California (UC); University of New Mexico (UNM); and Instituto Botánico, Ministerio de Agricultura y Cría, Caracas (VEN); The abbreviations of herbarium names are those of Lanjouw and Stafleu (Index Herbariorum, ed. 5, 1964) except for CHAP and IPN which are the author's.

This paper is based on a doctoral dissertation prepared at Yale University under the guidance of Dr. John R. Reeder, whose advice, encouragement, and perseverance will always be an inspiration to me. To his wife, Charlotte Goodding Reeder, my sincere appreciation for her assistance during the entire study at Yale. The work was completed at the U.S. National Herbarium and I am most grateful to Dr. Jason R. Swallen for his advice, assistance, and generosity in

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Historical Considerations

The description of the genus *Epicampes* by Jan S. Presl (1830) was based on a single collection from southern Mexico. In K. B. Presl's introduction is the statement (translated): "In the month of November Thaddaeus Haenke went alone to the capital city of Mexico, and returned in December to Acapulco." It was on this trip in 1791 that Haenke collected the type specimen of *Epicampes*. Although no locality other than "Mexico" is given, Presl's description and illustration of the specimen resemble most closely other specimens of *Epicampes* from the central Mexican plateau. Furthermore, Haenke's specimen was probably collected higher on the plateau in the state of Morelos or México, rather than in the lower and more tropical elevations of Guerrero, of which Acapulco is the main port of entry on the Pacific.

The name *Epicampes* may have been derived from the classical Greek word "*kampes*," an adjective meaning "curved." It is unclear why Presl chose a word with such a meaning as a name for this genus. Unfortunately, he gives no indication of its etymology in the original description.

The type species, *Epicampes strictus* Presl (*Muhlenbergia robusta* [Fourn.] Hitchc.), is widely distributed in the higher elevations from the state of Jalisco southward into Central America. His description of the genus, translated from the Latin, follows:

> Panicle contracted, in the form of a spike, with alternate solitary branches. Glumes two, ovate, convex, nerveless, subequal, obtuse, entire. Floret a little longer than the glumes. Glumes two, convex, ovate, the lemma surrounding the palea at its base, entire, with the median nerve extending into a straight awn from beneath the apex, the palea 2-nerved, very obtuse, enclosing the genitalia. Stamens 3. Ovary ovate, emarginate at apex. Styles 2. Stigmas divided into dense branchlets. Lodicules . . . caryopsis. . . . It seems to differ enough from *Agrostis* by the entire lemma and palea, with a straight awn neither twisted nor plicate, from *Apera* by the awned lemma. To this genus belong also *Agrostis pubescens* and *A. lanata*.

Of the several features that Presl enumerated for *Epicampes*, the nerveless condition of the glumes and the awn rising from just be-

low the tip of the lemma have been regarded by subsequent authors as important diagnostic characters for the genus.

As originally proposed, *Epicampes* comprised three species. Besides *E. strictus*, Presl included *Agrostis lanata* H. B. K. and *A. pubescens* H. B. K. These species had been described by Humboldt, Bonpland, and Kunth (1815) from specimens collected by Humboldt in the state of Guanajuato, north of where Haenke had collected. Three other species described in the same work, *Crypsis macroura*, *C. phleoides*, and *Podosaemum distichophyllum*, were later included in *Epicampes* by other workers. Thus, the species assigned to *Epicampes* had been described under the genera, *Agrostis*, *Crypsis*, and *Podosaemum*.

Kunth, who originally named the two Humboldt collections from Guanajuato as species of *Agrostis*, later accepted Presl's contention that they belonged to *Epicampes*. In 1833, Kunth's *Agrostographia* was published in Germany, where *Epicampes* was included in the Agrostideae, a tribe established by Kunth in 1815. Incorporated in this tribe were all grasses characterized by single-flowered spikelets:

> V. Agrostideae. Spikelets single-flowered, rarely with a rudimentary subulate flower above the other. Glumes 2, lemma and palea, membranaceous-herbaceous; lower often awned. Stigmas mostly spreading. Through *Muhlenbergia* affinities with *Stipa*.

Although recent research has demonstrated the unnaturalness of the Agrostideae as interpreted by Kunth, many contemporary taxonomists still recognize the tribe and place in it *Muhlenbergia*, including the Epicampes group.

Kunth's description of *Epicampes* was similar to Presl's. He placed the genus between *Cinna* L. and *Sporobolus* Brown, mentioning that it "differs from *Cinna* principally by its convex, non-keeled glumes." The genus *Muhlenbergia*, in which many recent authors have incorporated *Epicampes*, evidently was not considered by Kunth to be as closely allied, for he separates the two by several genera.

Trinius (1841) recognized *Epicampes* essentially as Presl and Kunth had before him but described the species in more detail and added one new species, *E. gracilis* (*Muhlenbergia lindheimeri* Hitchc.). He described the glumes as 1-nerved, in contrast to Presl's and Kunth's statements that the glumes are nerveless. Yet, in his description of *E. strictus* and *E. pubescens*, Trinius noted that the glumes are nerveless. The new species Trinius described was from Texas, the first of the group from the United States.

Until 1874 *Epicampes* was treated as comprising only four species, *E. strictus*, *E. lanatus*, *E. pubescens*, and *E. gracilis*, all with a habit and panicle similar to the first species that Presl described, and as a

genus ranging from southwestern United States (Texas) to southern Mexico. This concept of *Epicampes* was expanded by Grisebach (1874) in a description and discussion of the collections of Argentine plants of Professor Lorentz. In this work Grisebach described a new species, *E. coeruleus* (*Muhlenbergia angustata* [Presl] Kunth), with spikelike panicles, 1-nerved, awn-tipped glumes, and a long acute ligule. At the same time he transferred two other species with spikelike panicles to *Epicampes: Cinna phleoides* Kunth (based on *Crypsis phleoides* H. B. K.) and *C. stricta* Kunth (based on *Crypsis stricta* H. B. K.). By incorporating these species from Argentina into *Epicampes*, the range of the genus was considerably extended.

George Bentham (1881) in the first really critical comments concerning the generic limits of *Epicampes* recognized four subtribes within the Agrostideae, one, the Euagrosteae, included *Epicampes*. About 16 genera comprised this subtribe, of which he concluded:

> . . . the general character is a dorsal usually twisted awn on the flowering glume, the grain neither so closely enveloped in the fruiting glume as in Stipeae, nor so readily exposed as in Sporoboleae, and the spikelets usually small, loosely paniculate, very rarely condensed into a head as in Phleoideae; but there are exceptions to every one of these characters, and the limits of the larger genera are so vague as to render this portion of the genera of Gramineae the least satisfactory of the whole series.

Bentham stated that *Epicampes* was composed of "about 16 species,"[1] but that this number was possibly too large and most probably reducible by one-third, and that it "is a genus most embarrassing to the systematist; for it seems to connect *Muhlenbergia* and *Sporobolus* with *Agrostis*." One of the characteristics he regarded as distinctive of *Epicampes* was the long, narrow, dense panicle composed of numerous small spikelets. He differentiated *Epicampes* from *Muhlenbergia* by the awns on the lemmas which, when present in the former, are short and not quite terminal, while in the latter are longer and terminal. The dorsal position of the awn was one of the chief distinguishing features recognized by Presl in establishing the genus. Bentham distinguished *Epicampes* from *Sporobolus* by the fact that in the former the glumes are thinner and more membranous than the lemma and palea but in the latter they are thicker and less membranous. Bentham admitted his unfamiliarity with many of the

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[1] A survey of the literature reveals only 9 published species of *Epicampes* up to and including those described in Bentham's paper. For his estimate of 16 species, Bentham doubtless relied on Fournier's treatment of the group in *Mexicanas Plantas*. Although the title page was not printed until 1886, Fournier had sent copies to several botanists as early as 1880. In the first part of his "Notes" (p. 20) Bentham stated that Fournier had supplied him with a copy, remarking, "I feel bound, insofar as I am concerned, to treat it as having already taken date."

published species, adding that, "a further study may require considerable modification of the generic character and limits."

Following the example of Grisebach, Bentham included in *Epicampes* additional species with spikelike panicles. He transferred Fournier's *Crypsinna* and Kunth's *Cinna macroura* and *C. stricta* to *Epicampes macroura* (*Muhlenbergia macroura* [H.B.K.] Hitchc.). *Cinna macroura* Thurber was placed in *Epicampes* to become *Epicampes rigens* Benth. (*Muhlenbergia rigens* [Benth.] Hitchc.), a species closely related to *E. macroura.* The genus *Bauchea* Fourn., represented by a single Mexican species, *B. karwinskyi,* which Bentham had not seen, was also considered by him to be an *Epicampes* (although later synonymized with *Sporobolus wrightii* Munro ex Scribn.).

In Bentham and Hooker (1883) [2] four subtribes of the tribe Agrostideae are listed, with the genera enumerated under each. The four subtribes are: Stipeae, Phleoideae, Sporoboleae, and Euagrosteae. *Epicampes* was placed within Euagrosteae and *Muhlenbergia* in Stipeae. *Sporobolus,* considered by some as closely allied to *Epicampes,* was the basis of subtribe Sporoboleae.

Of the four subtribes listed, the Sporoboleae, containing the single genus *Sporobolus,* is distinctive in that the grain is not a true caryopsis but rather the seed is loose from the ovary wall (pericarp). Furthermore, the fruit is loosely enclosed within the lemma and palea and drops out easily; for this reason the popular name "dropseed" has been applied to the genus. The chief distinction of the Euagrosteae appears to be the position of the awn on the lemma, dorsal in some cases, "rarely arranged subterminally to a mucro, or variously awned" (Bentham, 1883). However, grasses with awned lemmas are also found in the Stipeae and Sporoboleae. The position of the awn on the lemma in the Euagrosteae does not easily separate this subtribe, and the Stipeae and Euagrosteae show no distinctive features to separate them clearly.

According to Bentham's description of *Muhlenbergia* (Stipeae), the major character to differentiate this genus from *Epicampes* (Euagrosteae) was the relatively small size of the glumes as compared with the lemma and palea. Yet, even here species are included with the glumes subequal to the floret. The awn of the lemma in *Epicampes* was stated as minute and subterminal, although in *Muhlenbergia* the awn was described only as "rarely obsolete." There was no reference to its position on the lemma. Although Bentham gave these contrasting characters for the two genera, none was distinctive enough to separate all species of *Epicampes* from all species of *Muhlenbergia.*

[2] The treatment of Gramineae in *Genera Plantarum* (1883) was produced by Bentham whose "Notes on the Gramineae" (1881) was based on observations made during its preparation.

Following the lead of previous authors, Vasey (1885) placed *Epicampes* in the Agrostideae. Employing the system of Bentham and Hooker, he included *Muhlenbergia* in the subtribe Stipeae and *Epicampes* in the subtribe Euagrosteae. According to Vasey's interpretation, the only essential character that differentiated the two subtribes was the position of the awn on the lemma. He said of the Stipeae, "beard of the flowering glume terminal," and of the Euagrosteae, "flowering glume usually with a more or less twisted dorsal awn; rarely mucronate or awnless." Like Bentham and Hooker, he included the genera *Agrostis*, *Polypogon*, *Arctagrostis*, and *Cinna* in the same group of Euagrosteae with *Epicampes*.

In his description of *Epicampes*, Vasey recognized three species: *E. distichophyllus* Vasey, *E. macroura* Benth., and *E. rigens* Benth. He stated that the spikelets of *Epicampes* are much like *Sporobolus* but contracted in a long, narrow, and dense panicle. He added,

> . . . Outer glumes somewhat unequal, membranaceous, convex on the back, scarcely keeled, obtuse, three-nerved; flowering glume mostly equalling the outer ones, sometimes three to five nerved, entire or sometimes awned from the apex; palet hyaline, about equalling the flowering glume, two nerved or two-keeled.

Vasey seems to have considered long dense panicles and glumes a little longer than the lemma as the important features of *Epicampes*. He erred, however, in stating that the glumes are 3-nerved; previous agrostologists had emphasized the nerveless or 1-nerved condition of the glumes in species of this group. He also said that the lemmas ("flowering glumes") are entire or awned from the apex, but did not recognize the dorsal position of the awn as a diagnostic feature. Nevertheless, in *E. distichophyllus* Vasey (*M. emersleyi* Vasey) the awn is clearly dorsal, or subterminal, rather than terminal.

Hemsley received a copy of Fournier's manuscript of *Mexicanas Plantas* before its publication and drew upon it in *Biologia Centrali-Americana* (1885). In the introduction, Hemsley remarked, "with regard to many of the new species described by Fournier which we have had an opportunity of examining, we consider them as varieties undeserving of distinctive names even." Hemsley's treatment included many of Fournier's species, and he comments that of the 16 species proposed up to that time, several were not distinguishable as such. The genus *Epicampes* followed *Sporobolus* in his treatment, in accordance with contemporary taxonomic opinion. Both Hemsley's and Fournier's works merely contain listings of genera and species, with a brief description of each species but no descriptions of the genera. Fournier and Hemsley followed the treatment of Gramineae as proposed earlier by Bentham (1881).

Hackel (1890) in *The True Grasses* (a translation by F. Lamson Scribner and E. Southworth) also followed Bentham and placed *Epicampes* in the Euagrosteae. Hackel mentioned 12 species in contrast to the 13 recognized by Fournier.

Vasey (1892) listed two species of *Epicampes*, *E. ligulatus*, described as new, and *E. rigens* Benth. (*Muhlenbergia rigens* [Benth.] Hitchc.). One species that Vasey included in the genus *Muhlenbergia*, *M. emersleyi* Vasey,[3] was later transferred to *Epicampes* by A. S. Hitchcock. Vasey's concept of the generic limits of *Epicampes* did not fully coincide with the general established concept, for he certainly would have included *M. emersleyi* within *Epicampes* if he had been familiar with the characters used to delimit the genus. Except for the glabrous lemmas of *E. ligulatus* and *E. rigens*, no characters would exclude them from his concept of *Muhlenbergia*—but, even then, under *Muhlenbergia* he remarked that the flowering glumes, or lemmas, are "frequently" pubescent below. Although Vasey recognized *Muhlenbergia* and *Epicampes*, he failed to select good characters to distinguish these two genera.

A key to nine species of *Epicampes* was given by Beal in 1896. In his discussion, Beal remarked that all species of *Epicampes* seemed near *Agrostis*, but some closest to *Cinna*, others to *Muhlenbergia*, and yet others to *Sporobolus*. He stated:

> . . . the chief general feature is the long narrow dense panicle with very numerous rather small spikelets, the awn of the floral glume, when it exists, much smaller than in *Muhlenbergia* and often not quite terminal; the unawned species are distinguished from *Sporobolus* by the fruiting glume and grain which are nearly those of *Agrostis*.

The notes on *Epicampes* by Marcus Jones (1912) point up the confusion that had developed in establishing the boundaries for *Epicampes*. Jones' conclusions, based solely on morphological observations, are corroborated to a large extent by anatomical studies made by the present author. Jones considered as the most important character of *Epicampes* the specialized awn of the lemma that arises from just below the tip, that is, dorsally or from an emarginate tip.

Although Jones erred in associating *Bealia mexicana* Scribn. (*Muhlenbergia biloba* Hitchc.), *M. argentea* Vasey, and *M. clomena* Trin. with *Epicampes*, he did recognize that certain other species associated with *Epicampes* belong to a separate group. This group includes the species with spikelike panicles, coarse ribbed leaves, and firm ligules. Jones followed Fournier in assigning such species to the genus *Crypsinna*. He also included *Epicampes macroura* Benth.

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[3] Vasey also listed another *Muhlenbergia*, *M. distichophylla* Kunth. The specimen referred to, however, was *M. emersleyi* and is not to be confused with *M. distichophylla* of Mexico and Guatemala.

in the genus, as Fournier had done, and further considered *E. rigens* Benth. to be a member.

Fournier originally established the genus *Crypsinna* based in part upon *Crypsis* H. B. K. and in part on *Cinna* Kunth (not L.), and included species with 1-flowered spikelets and dense spikelike panicles. Bentham chose to reduce *Crypsinna* to *Epicampes*, but Jones accepted Fournier's genus and did not recognize those species with spikelike panicles as belonging to *Epicampes*.

Hitchcock in 1914 and in earlier works recognized the genus *Epicampes*, although later he united it with *Muhlenbergia*. His description of *Muhlenbergia* indicated that "it grades on the one hand into *Sporobolus*, from which it differs in having an awned or mucronate lemma, and on the other into *Epicampes*, from which it differs in having a relatively firmer lemma." Bentham used the firm lemma in *Epicampes* as a character in contrast with the thinner lemmas of *Sporobolus*.

Hitchcock (1920) based his description of *Epicampes* on the characters of the equal glumes, the awn of the lemma which, when present, characteristically rises from just below the tip, the caespitose, perennial habit of the plants, and the open, narrow, or spikelike panicles. Hitchcock regarded *Crypsinna* as a synonym of *Epicampes*. He also transferred *Muhlenbergia emersleyi* Vasey and *M. vaseyana* Scribn. (*M. distichophylla* sensu Vasey) to *Epicampes*, bringing the number of species to 15.

Bews (1929) regarded the texture of the lemmas as a significant character in differentiating genera within the Agrostideae. Under the first category of the tribe, "lemma usually hyaline or membranaceous at maturity, at least as delicate as the glumes, or more so," he included *Sporobolus*, *Agrostis*, and *Epicampes*, in addition to many other genera. *Muhlenbergia* is found under the second category, "lemma indurated at maturity, or at least firmer than the glumes." Bews listed the same species of *Epicampes* that Hitchcock had listed in his 1920 publication.

A significant change was made in the disposition of *Epicampes* by Hitchcock in 1934. In transferring *Epicampes ligulatus* Scribn. to *Muhlenbergia* (*M. longiligula* Hitchc.), he commented:

> . . . the character which I have used to differentiate the two, the awn from the back of the lemma, just below the apex in *Epicampes* and from the tip in *Muhlenbergia*, has several exceptions in the latter genus. Since it is impossible to find a clear line of division to separate the genera, I am uniting *Epicampes* with *Muhlenbergia*.

Hitchcock (1935) contributed a complete treatment of all North American species of *Muhlenbergia*, in which he transferred all species

of *Epicampes* to *Muhlenbergia*. His disposition of the group has been followed subsequently by most American taxonomists.

The inclusion of *Epicampes* within *Muhlenbergia*, however, has not been universally accepted. The most recent system of classification of the grasses treating all known genera was that of Robert Pilger in 1954, with a more complete form in 1956. Pilger placed *Epicampes* in the tribe Eragrosteae which he divided into six subtribes. Subtribe 5, Sporobolinae, included not only *Sporobolus*, but also *Epicampes*, *Crypsis*, *Heleochloa*, *Urochondra*, *Sphaerocaryum*, and *Blepharoneuron*. *Muhlenbergia*, excluding the *Epicampes* species, formed subtribe 6, the Muhlenbergiinae. A translation of the section of his key separating the Sporobolinae and Muhlenbergiinae follows:

I. Spikelets often broad; glumes thin; lemmas awnless; caryopsis more or less wide . . . . . Subtribe 5. SPOROBOLINAE

II. Spikelets small; glumes firm; glumes often more or less shorter than the lemmas, these often more or less long-awned; caryopsis small, cylindrical. Subtribe 6. MUHLENBERGIINAE

Pilger did not enumerate the species he recognized under *Epicampes*, but most of the species traditionally regarded as members of this genus possess awned lemmas. The type specimen of the genus, *E. strictus* Presl, is figured with short-awned lemmas. Moreover, since Presl established *Epicampes* the position of the awn on the lemmas has been used as a generic character of great importance. It is therefore surprising that Pilger should have placed *Epicampes* in a tribe composed of members with awnless lemmas.

Hubbard, in his treatment of Gramineae (1959, rev.), recognized *Epicampes*. *Sporobolus*, often regarded as showing a relationship with *Epicampes*, was placed in the tribe Sporoboleae, along with *Blepharoneuron*. *Muhlenbergia* and *Epicampes*, in addition to *Agrostis*, *Calamagrostis*, *Lagurus*, *Gastridium*, *Triplachne*, *Echinopogon*, *Dichelachne*, *Polypogon*, *Phleum*, and *Alopecurus*, among others, constituted the tribe Agrosteae.

It is apparent that *Epicampes* never has been clearly understood. Different characters have been used by botanists to delineate the genus and few of their descriptions fully agree. The American, A. S. Hitchcock, incorporated the species of *Epicampes* into the genus *Muhlenbergia*, and since then most American taxonomists have accepted his treatment.

Leaf Anatomy and Epidermis

The first suggestion that the anatomy of grass leaves might be useful in systematics was made by Duval-Jouve (1875) who found differences in the distribution of bulliform cells among species of different tribes. Additional anatomical differences were pointed out by Schwendener (1890). In 1898, Pée-Laby recognized five groups

based on characters of leaf anatomy, although these groups were based on poor characters (Brown, 1958). Avdulov's system (1931) incorporated the characters of leaf anatomy and chromosome size and number. Prat (1936) found that characters of the leaf epidermis are useful from a systematic standpoint and that the results based on these characters correlate well with those derived from a study of the internal anatomy. He referred to Avdulov's major groups as "panicoid" and "festucoid" and segregated the former into two subgroups, the "eupanicoid" and "chloridoid."

Brown (1958), in a study of the leaf anatomy of 101 species in 72 genera, found that six groups can be delimited by characters of the internal anatomy. Various combinations of these characters make it possible to differentiate the six basic groups that Brown designated bambusoid, festucoid, arundoid, panicoid, aristidoid, and chloridoid.

Tateoka et al. (1959) surveyed the leaf epidermis of 238 species of grasses and found that two groups, which differ in the type of microhairs present, correspond to the panicoid and chloridoid groups of Prat. They also reported that the bicellular microhairs of several genera have distinctive features which suggest that leaf epidermal characters may be useful at the generic level.

The most detailed survey of leaf anatomy and epidermis of grasses was made by Metcalfe (1960). He compiled the diagnostic features of the leaf epidermis and internal anatomy of 206 genera, representing 413 species. In addition, he included information on numerous other species, summarized from the literature. The survey by Decker (1964) of 135 genera traditionally placed in the tribe Festuceae demonstrates the value of leaf anatomy in reinterpreting a large, long-recognized tribe.

In the present study, the leaf anatomy and epidermis were studied by the author in about 50 species of *Muhlenbergia*, including those traditionally placed within *Epicampes*. About 50 additional species of *Muhlenbergia* were studied by Reeder at Yale University, and the author was fortunate to have the results of Reeder's unpublished studies for comparison with his own findings.

LEAF ANATOMY

Comparative studies of leaf anatomy were made from transverse sections of leaves of herbarium specimens. Mature blades were selected from about the middle of the culm and sections taken from a point in the blade approximately 1 cm. from the ligule (at this point the vascular bundles and associated structures are well developed; more distally the blades become narrower and certain features become altered). The dry blade was placed in boiling water for several minutes to soften and to bring it back as much as possible to the

pliable condition of a fresh leaf. In some cases the blades were soaked in a 0.3–0.4 percent solution of trisodium phosphate in a 60° paraffin oven for 1½–2 hours, although equally good results were obtainable without this additional treatment.

Freehand sections were made in all cases. The leaves were heavily sclerified and their rigidity permitted thin sections to be made by hand, thus obviating the use of a microtome. The blade was placed between halves of a block of celloidon and sections cut with a sharp single-edged razor blade. The sections were stained with Chlorazol Black E for ½ hour and then washed and brought through the alcohol series to absolute ethyl alcohol, and made permanent by mounting in diaphane.

Muhlenbergia species traditionally treated as *Epicampes* possess panicles that are either spikelike or open and pyramidal or columnar. The leaves in the former group become inrolled upon drying (*M. rigens*); in the latter group the leaves become folded upon drying (*M. gigantea*). Anatomical studies of the leaves of those two species reveal striking structural differences and the leaves of the other species of the Epicampes group are of one type or the other. For purposes of discussion, species with the leaf anatomy of *M. rigens* are referred to as having a "Rigens" type, and species with a leaf anatomy of *M. gigantea* are referred to as having a "Gigantea" type.

Plates 4–14 contain photomicrographs of leaf cross sections of a number of species of *Muhlenbergia*, including those of the Epicampes group. A partial leaf cross section of *M. rigens* appears in plate 5, figures 1 and 2, and of *M. gigantea* in plate 7, figure 2. The anatomical features of Epicampes leaves are illustrated on plate 4 in cross sections of *M. lindheimeri* and *M. palmeri* leaves. These two species have a leaf anatomy that corresponds, respectively, to that of *M. gigantea* and *M. rigens*.

Anatomical Structure of Leaves of the Epicampes Group [4]

UNITS: The leaf consists of a series of units of varying sizes, each unit representing a single rib of the leaf. The individual unit contains a vascular bundle and associated structures between and including the upper and lower epidermis.[5] On plate 4, figure 2 are

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[4] The author is grateful to Dr. C. R. Metcalfe of the Royal Botanic Gardens, Kew, for his aid in interpreting the anatomical structures of the cross section of the leaf of *M. lindheimeri* from the photomicrograph sent to him.

[5] I am employing the term "unit" as used by Brown (1958, p. 176) to describe leaves of chloridoid grasses—"In these groups each bundle, sheath, and associated radial chlorenchyma constitute a discrete unit of structure separated from the similar adjacent units by large, empty, bulliform cells"—but I consider also the upper and lower epidermis and include sclerenchyma as part of this unit. The words "primary," "secondary," and "tertiary" to distinguish units are mine.

shown four units of a blade of *Muhlenbergia lindheimeri* and below, figure 3, seven units of a blade of *M. palmeri.*

Units are designated primary (1°), secondary (2°), and tertiary (3°), from largest to smallest. In the Gigantea type, only 1° and 2° units are found. The median unit is heavily sclerified at the base. This 1° unit and adjacent units are "embedded" in a mass of parenchyma, the whole arrangement constituting the "midvein area," or keel. The keel structure is shown on plate 4, figure 1. The 1° units alternate with one to three 2° units throughout the leaf. In the Rigens type, 3° units often are present, in addition to 1° and 2° units. As seen in *M. palmeri* one 2° and two 3° units occur between the two 1° units. Such an alternation of units occurs throughout the leaf and the central units are not specialized into a keel.

VASCULAR BUNDLES: The phloem of the 1° vascular bundles of *M. lindheimeri* and *M. palmeri* appears as darkly-stained groups of cells among nonstained thick-walled cells. All of the phloem is darkly stained in the 2° and 3° bundles of these species. The phloem of the 1° bundles is sclerosed, i.e., partly converted to lignified fibers. In cross section the active parts of the phloem (sieve tubes and parenchyma) appear as darkly-stained strands embedded in a fibrous ground tissue that is not stained. Sclerosis of the phloem is less pronounced, or lacking, in the 2° and 3° bundles.

The xylem of the 1° bundles is characterized by large metaxylem vessels on either side of the protoxylem. (The line marking the xylem in the photomicrograph of *M. palmeri*, plate 4, points to the metaxylem.) These large metaxylem vessels are lacking in the 2° and 3° bundles; in these bundles both the xylem and phloem stain black and are indistinguishable in the photomicrographs.

The 1° units are defined as those having metaxylem vessels, which are lacking in the 2° and 3° units. In cases where the 1° and 2° units are about equal in size, they are distinguished on the basis of whether or not they possess such metaxylem vessels.

BUNDLE SHEATHS: Two distinctive layers of cells, or "sheaths," surround the vascular bundle. The innermost, variously termed the "mestome sheath," "inner sheath," or "endodermis" is composed of thick-walled cells. The cells of the inner sheath adjacent to the xylem are larger; the cells adjacent to the phloem fibers are smaller and often indistinguishable from the latter.

The inner sheath is surrounded by a single layer of conspicuously larger, thin-walled cells, termed the "parenchyma sheath" or "outer sheath." The outer sheath may be continuous around the inner sheath, or interrupted below, above, or both. In the 1° units of *M. lindheimeri* the outer sheath is interrupted above and below, but only above in the 2° units. It is continuous in the 2° and 3° units

of *M. palmeri*. (The closed condition is typical of every unit of the leaf in some species of *Muhlenbergia*—cf. plate 12, figures 1, 2, and plate 13, figure 1.)

CHLORENCHYMA: The chlorenchyma lies adjacent to the outer sheath and both are stained black in the photomicrograph. Although not evident in the photomicrograph, the cells are radially arranged. The chlorenchyma assumes the same pattern as the outer sheath in the unit, being continuous around the inner sheath or interrupted. (Photosynthetic activity is confined to this narrow layer of chlorenchyma and, presumably, the outer sheath also; together, they constitute a relatively small part of the whole unit [Brown: 1958, p. 176]).

SCLERENCHYMA: The individual units, especially the 1° ones, possess caps of sclerenchyma cells subjacent to the upper and lower epidermis. The amount of sclerenchyma varies, but it is especially well developed at the base of the central unit where it reinforces the keel of the blade. In a species with the Rigens type of leaf anatomy the sclerenchyma often forms a continuous layer subjacent to the lower epidermis.

THICK-WALLED PARENCHYMA: Between the vascular bundle and subepidermal sclerenchyma is a mass of large parenchymatous cells. They are referred to here as "thick-walled" parenchyma,[6] as the walls of these cells appear to be thicker than in normal parenchymatous cells. These cells constitute a large part of the 1° units, a smaller part of the 2° units, and are lacking in the 3° units.

In some cases the thick-walled parenchyma of the units is confluent between them. Such a condition is found in the keel of leaves of the Gigantea type in which the vascular bundles and surrounding sheaths give the appearance of being embedded in a mass of parenchyma cells. In such cases there is no observable difference between parenchyma cells of the units and those that occur between them as they are confluent.

COLORLESS CELLS: Between the units are found one to several rows of cells that look similar to thick-walled parenchyma. Metcalfe refers to these as colorless cells. In some grasses bubble-like cells that are part of the epidermis are referred to as bulliform cells. Technically, the cells marked (bc) in the photograph of *M. lindheimeri* are bulliform cells. The cells subjacent to these bulliform cells are the colorless cells (cc). In species of the Epicampes group

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[6] According to Metcalfe (personal communication), "It is quite in order to refer to the cells as thick-walled parenchyma unless they can be shown in l.s. to be appreciably longer than wide. Even if they are somewhat elongated it is best to refer to them as 'elongated parenchymatous cells' as they are not fibrous or sclereids."

there is no obvious difference between the bulliform and colorless cells apart from the position they occupy.

The Rigens and Gigantea Types of Leaf Anatomy

The leaf anatomy of the following species, traditionally placed in *Epicampes*, was examined: *Muhlenbergia distans*, *M. distichophylla*, *M. emersleyi*, *M. gigantea*, *M. grandis*, *M. lindheimeri*, *M. longiligula*, *M. macrotis*, *M. macroura*, *M. pubescens*, *M. rigens*, *M. robusta*, *M. speciosa*, and *M. virletii*.

All the above species possess the following anatomical features: (1) The phloem of the 1° vascular bundles is partly sclerosed. (2) The vascular bundle is surrounded by an inner sheath and an outer sheath. Adjacent to the outer sheath is the chlorenchyma, appearing under high power to consist of a layer of narrow cells, radially arranged. (3) A large amount of thick-walled parenchyma occurs adaxial, sometimes abaxial, to the vascular bundle. (4) A thick cap of sclerenchyma lies below the upper and lower epidermis of the 1° units. Apart from shape, the units of all species of *Epicampes* are of similar structure. The major differences are in the kinds of units present and in their arrangement.

The Rigens type of leaf anatomy is characterized by the following features: (1) A similar alternation of units occurs throughout the leaf. The 1° units alternate with one or two 2° units or three to five smaller units (consisting of two to four 3° units and a 2° unit). There is no differentiation of central units into a keel. (2) The lower surface of the blade is flat, or ribbed and furrowed; the upper surface is ribbed and furrowed. (3) The 1° units are rounded above in *M. macroura* (cf. *M. dubia*, pl. 5, fig. 3), obtriangular in *M. rigens* (pl. 5, figs. 1, 2), and in some species more or less rectangular (e.g., *M. elongata*, pl. 11, fig. 2).

The following species of the Epicampes group possess a Rigens type of leaf anatomy: *M. macroura* and *M. rigens*.

The Gigantea type of leaf anatomy is characterized by the following features: (1) Only 1° and 2° units are present. The central units of the blade are specialized into a keel. The thick-walled parenchyma of these units is confluent and a large cap of sclerenchyma is developed at the base of the central unit. (See *M. gigantea*, pl. 9, fig. 1, for illustrations of the central and adjacent units of the keel.) Beyond the midrib area is a regular alternation of 1° and 2° units. The 1° units are separated by one to three 2° units. (2) The upper and lower surfaces of the blade are ribbed and furrowed. Beyond the midrib area the units are separated by several layers of colorless

cells. The sclerenchyma subjacent to the lower epidermis is confined to the individual units and therefore does not form a continuous layer between them. (3) The 1° units are more or less rectangular. The central 1° unit of the keel is rounded or obtuse below.

The following species of the Epicampes group possess a Gigantea type of leaf anatomy: *M. distans*, *M. distichophylla*, *M. emersleyi*, *M. gigantea* (pl. 7, fig. 2, and pl. 9, fig. 1), *M. grandis*, *M. lindheimeri* (pl. 7, fig. 3, and pl. 8, fig. 3), *M. longiligula* (pl. 10, fig. 1), *M. macrotis* (pl. 7, fig. 1), *M. pubescens*, *M. robusta*, *M. speciosa*, *M. virletii*.

The Rigens or Gigantea Type in Species of *Muhlenbergia*

Apart from the anatomical differences that separate the species of the Epicampes group into the Rigens and Gigantea types, the two groups have the same basic unit structure in the leaves and share the following gross morphological features: Plants perennial, caespitose (usually strongly so); culms erect, not branching at the nodes; and panicle usually densely flowered.

The species with a Rigens type of leaf anatomy have rounded basal sheaths, a firm ligule, and the leaves become inrolled upon drying. In contrast, most species with a Gigantea type of leaf anatomy have compressed-keeled basal sheaths, a membranous ligule, and the leaves become folded upon drying.

Many species of *Muhlenbergia* share the morphological features common to all of the species of the Epicampes group. These species may be grouped into those having compressed-keeled basal sheaths and a membranous ligule, and those with rounded basal sheaths in association with a firm ligule. Because of the close morphological similarities to the Epicampes group, a study of the leaf anatomy was made, with the following results:

Muhlenbergia species with the Rigens type of leaf anatomy:

M. angustata
M. arenicola
M. articulata
M. capillaris (pl. 10, fig. 2)
M. dubia
M. dubioides
M. elongata (pl. 11, fig. 2)
M. expansa (pl. 6, fig. 2)
M. firma
M. glabrata
M. holwayorum
M. jaliscana
M. lucida
M. metcalfei
M. nigra
M. reverchonii (pl. 11, fig. 1)
M. rigida
M. setifolia
M. subaristata
M. xerophila

All of the above species have rounded basal sheaths and a firm ligule. (The rather variable species *M. rigida* sometimes may have a long membranous ligule.)

Species that have the Gigantea type of leaf anatomy:

M. aurea
M. breviligula
M. gooddingii
M. inaequalis
M. involuta
M. iridifolia
M. lehmanniana
M. longiglumis (pl. 10, fig. 3)
M. mutica
M. pubigluma
M. reederorum
M. scoparia
M. versicolor
M. xanthodas

These species have compressed-keeled basal sheaths and membranous ligules with the exception of *M. involuta* and *M. reederorum* in which the sheaths are rounded (rarely compressed) and ligules firm below and membranous above.

Some species of *Muhlenbergia* exhibit certain anatomical features that require special mention:

M. longiligula (pl. 10, fig. 1). The several 1° units of the midrib area are of equal size. The central unit does not possess a larger basal cap of sclerenchyma than the adjacent units of the keel. The basal sheaths are either rounded or sometimes compressed, but never strongly keeled. However, the structure of the units, the sclerosed phloem of the 1° bundles, and the midrib area of thick-walled parenchyma are characteristic of the Gigantea group of species.

M. longiglumis (pl. 10, fig. 3). The central unit is a 1° bundle with sclerosed phloem and a large basal cap of sclerenchyma; both are characters of the Gigantea type of leaf anatomy. The central units, however, are not embedded in a mass of thick-walled parenchyma. On the basis of leaf anatomy, this species does not conform well to either anatomical type but shows more similarity to the Gigantea type.

M. aff. *montana* (pl. 11, fig. 3). The units have an arrangement similar to that of the Rigens type. However, the phloem of the 1° units is not sclerosed.

M. involuta. All of the units of the leaf are embedded in a continuous layer of thick-walled parenchyma, unlike the Gigantea species in which such a condition is confined to the keel. The phloem of the 1° bundles is sclerosed and the central units possess a large basal cap of sclerenchyma, as in the Gigantea type. The anatomy of the leaf most closely approaches the Gigantea type.

M. stricta. The units are all very large and are connected by a continuous layer of thick-walled parenchyma and the phloem of the 1° bundles is sclerosed. The central unit does not possess an additional amount of basal sclerenchyma. On the basis of leaf anatomy this species exhibits greater similarity to the Gigantea type, but its gross morphology is more like that of species in the Rigens group.

M. torreyana (pl. 9, fig. 3). The leaves of this species have a keel structurally like that of the Gigantea group, but the phloem of the 1° bundles is not sclerosed. Morphologically it is unlike species of the Gigantea group in having short, very scaly rhizomes and branching culms, and a minute, ciliate, firm ligule.

Muhlenbergia Species Unlike the Rigens and Gigantea Types

Most species of *Muhlenbergia* have a leaf anatomy quite different from the Gigantea and Rigens types. Although the anatomical structure of all cannot be discussed here, several points should be mentioned to illustrate how these species compare with the Epicampes group and allies.

Photomicrographs of 11 species of *Muhlenbergia* with a leaf anatomy distinct from the Rigens or Gigantea types are shown on plate 9, figure 3, plate 11, figure 3, and plates 12–14.

All 11 of these species of *Muhlenbergia* differ from species of the Rigens and Gigantea types in the condition of the phloem. The phloem of all the bundles, including the 1° ones, when these are differentiated, is darkly stained throughout, indicating it is completely functional and not sclerosed. Special reference is made to *M.* aff. *montana* (pl. 11, fig. 3) and *M. torreyana* (pl. 9, fig. 3). In these species the 1° units are similar to those of the Epicampes group but the phloem of the 1° units is not sclerosed.

The annual species are characterized by a relatively simple unit structure, with little additional sclerenchyma or thick-walled parenchyma. Note, for example, the annuals *M. confusa* (pl. 13, fig. 1), *M. crispiseta* (pl. 14, fig. 1), *M. peruviana* (pl. 12, fig. 1), and *M. pulcherrima* (pl. 12, fig. 2). In *M. peruviana* and *M. pulcherrima* the units are of equal size; the outer sheath and chlorenchyma are continuous above. Additional sclerenchyma and parenchyma are lacking in the units and the phloem is not sclerosed. *M. crispiseta* has sclerenchyma developed in the central unit and some in each of the other units. The outer sheath and chlorenchyma entirely circle the vascular bundle without interruption and the phloem in the bundles is not sclerosed.

Among perennial Muhlenbergias, plates 12–14, are *M. arizonica* (pl. 12, fig. 3), *M. asperifolia* (pl. 14, fig. 2), *M. plumbea* (pl. 13, fig. 3), and *M. richardsonis* (pl. 13, fig. 2). The structure of the individual units in *M. richardsonis* and *M. asperifolia* approaches that of the Epicampes group in its specialization. However, the phloem of the 1° bundles in these two rhizomatous perennials is not sclerosed. *Muhlenbergia plumbea,* another rhizomatous perennial, has units mostly equal in size, except for the central unit which has a basal

cap of sclerenchyma. Note that the outer sheath and chlorenchyma are continuous around the vascular bundles. The phloem of the bundles is not sclerosed. The leaf of *M. arizonica*, a perennial that branches at the nodes, is not too unlike that of *M. plumbea*. The units are mostly equal in size, and the median one is heavily sclerified. The outer sheath and chlorenchyma are continuous around the vascular bundles outside of the central unit. The phloem of the vascular bundles is not sclerosed.

Various anatomical configurations in the leaves of the remaining species of *Muhlenbergia* examined are not illustrated here.[7] In all of these species the phloem of the vascular bundles is not sclerosed.

Conclusions

The leaves of species traditionally placed in *Epicampes* are characterized by an inner sheath (or endodermis), a parenchyma (outer) sheath, and chlorenchyma, consisting of cells radially arranged. All are features of the chloridoid type of leaf anatomy, as pointed out by Brown (1958). On the basis of leaf anatomy these species are allied to *Muhlenbergia*, *Sporobolus*, *Lycurus*, and other genera of the chloridoid alliance. In contrast, the leaves of *Agrostis* and *Cinna* are of the festucoid type, as Brown has shown, and therefore do not show a relationship to *Epicampes*. On the basis of leaf anatomy, *Epicampes* should be removed from the Agrostideae and placed with other members of the chloridoid alliance. The present investigations have shown that *Epicampes* is most closely related to species of *Muhlenbergia* which not only have similar gross morphological features, but leaf anatomical features; most noteworthy is the unique condition of sclerosed phloem in the 1° vascular bundles. These findings support those of Schwabe (1949) who in a study of the foliar anatomy of 22 species of *Muhlenbergia*, including two species of the Epicampes group, concluded that the latter should probably be included in the former.

LEAF EPIDERMIS

Sections were taken from the upper and lower epidermis of the leaf. In all cases the preparations were made from leaves taken from herbarium specimens. Sections of the blade, 1–1½″ long, were placed in boiling water until softened, just as in preparing

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[7] The reader is referred to the treatment of Schwabe (1949) in which features of the leaves of many additional species of *Muhlenbergia* are illustrated.

the whole leaf for cross sections. To remove the epidermis of the abaxial surface the blade was placed with the abaxial surface down on a clean glass slide. With the aid of the 10 × power of a binocular microscope, the tissue of the leaf was scraped away with a scalpel until only the epidermis remained. The same process was repeated for the adaxial surface with the adaxial surface down.[8] The epidermal scrapes were stained with methylene blue and counterstained with ruthenium red. They were then washed in water to remove the excess dye, brought through the alcohol and xylene series, and mounted in Permount.

Constituents

The epidermis of the grass leaf contains a number of different cell types, among them microhairs, prickle-hairs, papillae, long cells, stomatal cells, interstomatal cells, and silica cells. The bicellular microhairs [9] and silica cells exhibit the greatest differences between the groups of species within Epicampes.

MICROHAIRS: All species studied of *Muhlenbergia* (including *Epicampes*) have bicellular microhairs. Differences are found in the shape and in the ratio of the length of the basal to the upper (distal) cell. In some species the microhairs are short and broad; the basal cell is equal to, or a little longer than, the distal cell. In other species the microhairs are longer and narrower, and the basal cell is much longer than the distal cell.

SILICA CELLS: Silicon-containing cells in the epidermis are referred to as "silica cells" or "siliceous cells." Characterized by a wall heavier than that of adjacent cells with small granules within the cell, they occur in rows and are a major constituent of the epidermis in species of the Epicampes group. In some species all of the silica cells are saddle-shaped and rather simple in outline; in others most of them are dumbbell- or cross-shaped; in still others the majority are saddle-shaped, with cross-shaped cells occurring infrequently among them.

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[8] In many species, e.g., *M. macroura*, the blade is characterized by a flat abaxial surface and an adaxial surface of ribs and furrows. In such cases the whole epidermis scrapes off easily from the abaxial surface but only strips of epidermis can be removed from the adaxial surface, representing the top surfaces of the ribs only.

[9] Metcalfe (1960, p. xliii) remarks, "Micro-hairs are not always easy to examine, but it is generally rewarding to persevere with them because they are valuable indicators of the affinities of the grasses in which they occur."

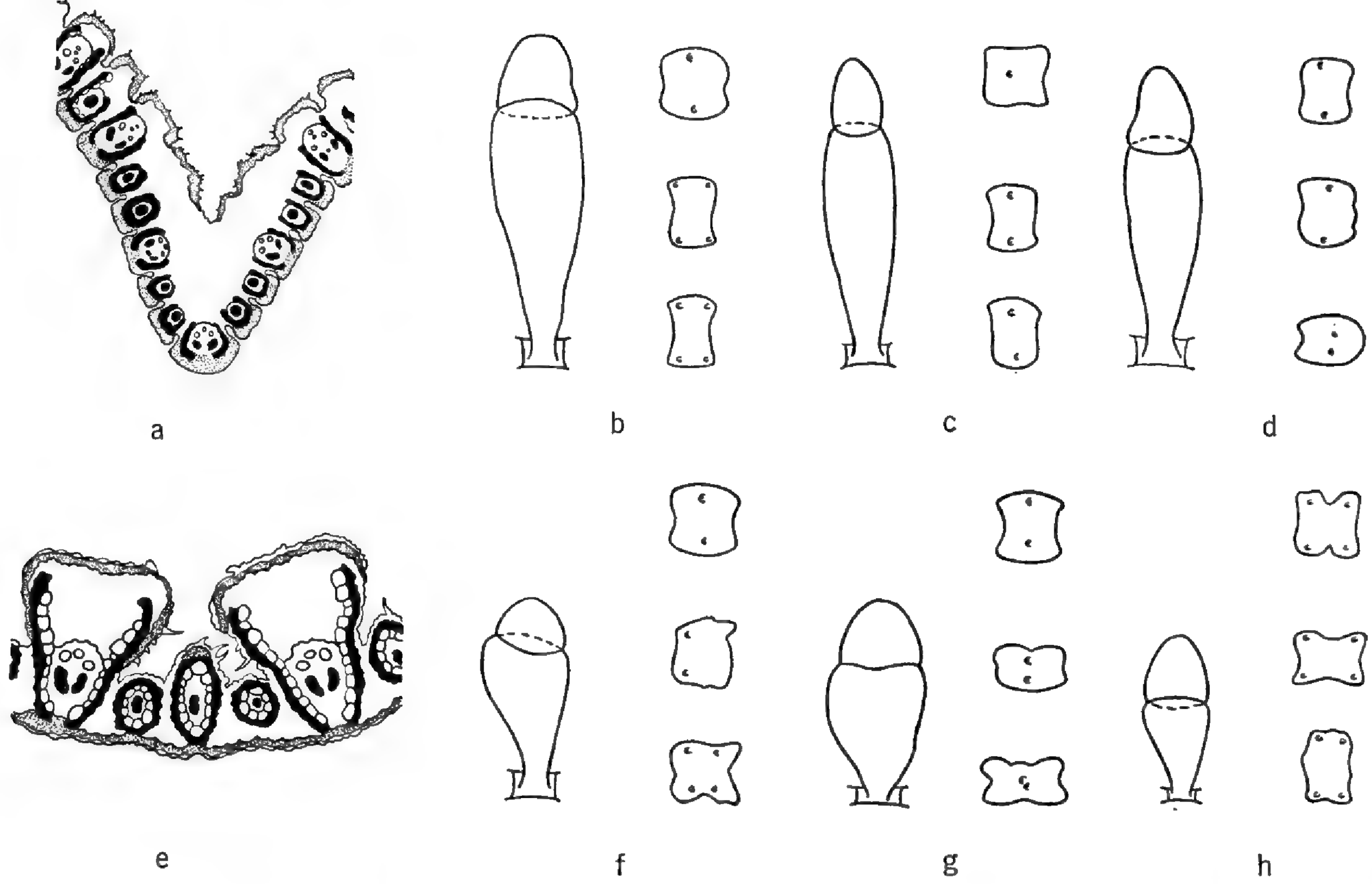

FIGURE 1.—Bicellular microhairs and silica cells. *a–d*, Species of section *Epicampes: a*, Diagrammatic cross section of the leaf of *Muhlenbergia lindheimeri; b*, *M. pubescens* (*Soderstrom* 692); *c*, *M. gigantea* (*Reeder & Reeder* 2488); *d*, *M. macrotis* (*Mexia* 9098). *e–h*, Species of section *Podosemum: e*, Diagrammatic cross section of the leaf of *M. rigens; f*, *M. rigens* (*Reeder & Reeder* 2662); *g*, *M. dubioides* (*Soderstrom* 931); *h*, *M. macroura* (*Matuda* 2829). These are all diagrammatic and are not drawn to scale.

Following is a summary from epidermal studies in Epicampes species:

Species	*Average ratio of basal to distal cell of microhair*	*Shape of silica cells:* s = *saddle-shaped* x = *cross-shaped* d = *dumbbell-shaped*
M. distans	6.6:1	s
M. distichophylla	5.1:1	s
M. gigantea	4.0:1	s
M. grandis	3.2:1	s
M. lindheimeri	–	s
M. macrotis	5.7:1	s
M. macroura	2.2:1	mostly x or d
M. pubescens	4.7:1	s
M. rigens	2.3:1	mixed, s and d
M. robusta	4.3:1	s
M. speciosa	–	s
M. virletii	4.0:1	s

Species of the Epicampes group with a Rigens type of leaf anatomy (*M. macroura* and *M. rigens*) exhibit certain characteristics in their epidermis different from the other species of Epicampes. The bicellular microhairs are short and broad in these species and silica cells are dumbbell-shaped, cross-shaped, or saddle-shaped. In the species that have a Gigantea type of leaf anatomy, the bicellular microhairs are generally long and narrow, and the upper cell is usually much shorter than the basal cell. In these species the silica cells are always saddle-shaped.

The epidermis of other species of *Muhlenbergia* with a Rigens or Gigantea type of leaf anatomy also was studied. In these, likewise, the epidermis of members with a Gigantea type is characterized by mostly long and narrow bicellular microhairs and rectangular or saddle-shaped silica cells. And in the epidermis of species with a Rigens type the silica cells are cross-shaped, saddle-shaped, or rectangular, and the bicellular microhairs relatively short and broad. In figure 1 are illustrated the major types of silica cells and bicellular microhairs encountered.

Conclusions

Epidermal features of the species of *Muhlenbergia*, including *Epicampes*, are panicoid in nature; microhairs are present and the silica cells are rectangular, saddle-shaped, cross-shaped, or dumbbell-shaped. Relationship with the chloridoid group is apparent in the club-shaped or globose microhairs and membranes of equal thickness on the upper and lower cells (Prat, 1936; Tateoka, Inoue, and Kawano, 1959; Metcalfe, 1960).

The Embryo

Until recently the structure of the grass embryo has been of passing interest to grass taxonomists. Bruns (1892), who dealt with about 60 species, was the first worker to publish on grass embryos. Later, Van Tieghem (1897) and Kennedy (1899) added to the understanding of the grass embryo, the work of the former being more significant from the standpoint of systematics. Not until Yakolev (1950) and Reeder (1953) was the value of the embryo in grass systematics again stressed. Reeder (1957) in a paper of great significance presented his findings based on a study of the caryopses of about 300 species of grasses. These included over 150 genera, representing all of the tribes in the traditional Hackelian system. Reeder showed that several embryo groups could be recognized, and the criteria he used to distinguish them are the relative size of the embryo to endosperm in the caryopsis, as well as the features observable in the transverse and median sagittal sections of the embryo. He listed six groups of grasses based on various combinations of four embryo characters: festucoid, panicoid, chloridoid-eragrostoid, bambusoid, arundinoid-danthonioid, and oryzoid-olyroid. Reeder later (1962) reinterpreted the oryzoid-olyroid genera as bambusoid but segregated a further group, the centothecoid.

In the present study, mature caryopses were selected from herbarium specimens, placed in boiling water for a few minutes, then soaked overnight in FAA. They were then transferred to a 3 percent solution of KOH for 1–2 hours to soften the endosperm. After removing the endosperm, the embryo was embedded in agar and the agar block, containing the embryo, run through the butyl alcohol series and embedded in paraffin. Serial sections 10μ in thickness were made, transversely and longitudinally, in the sagittal plane. Safranin and Fast Green were used in staining.

Embryos of 10 species of *Muhlenbergia* were sectioned, of which 9 species have been traditionally associated with *Epicampes*. Of these, 7 have a Gigantea type of leaf anatomy: *M. emersleyi*, *M. gigantea*, *M. grandis*, *M. longiligula*, *M. macrotis*, *M. pubescens*, and *M. robusta*. All are illustrated in figure 2 except *M. emersleyi*. Two have a Rigens type: *M. macroura* (fig. 3) and *M. rigens* (fig. 2). Additional species, represented in figure 3, are *M. nigra*, with a Rigens type, and *M. schreberi*, the type species of *Muhlenbergia*. For comparison, diagrams also of the embryos of five genera that have been suggested as bearing a relationship to *Epicampes* appear in figure 3: *Agrostis*, the type genus of the classical tribe Agrostideae, *Cinna*, *Polypogon*, *Sporobolus*, and *Stipa*.

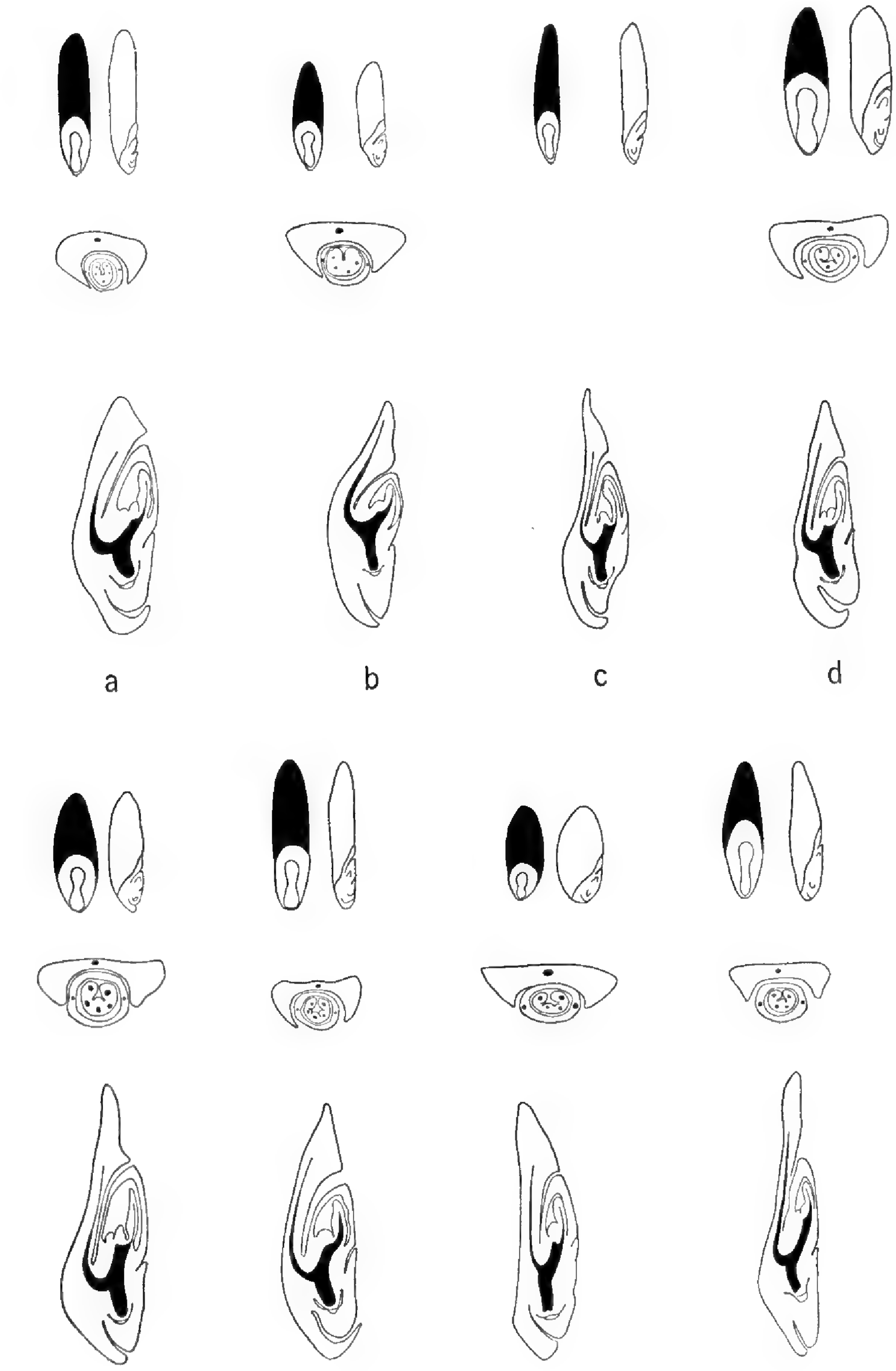

FIGURE 2.—Outline drawings of caryopses, median sagittal sections, and transverse sections through the coleoptile region of *Muhlenbergia* embryos: *a*, *M. macrotis* (*Pringle* 2360); *b*, *M. robusta* (*Standley* 59136); *c*, *M. robusta* (*Pringle* 2321); *d*, *M. grandis* (*Pringle* 2765); *e*, *M. gigantea* (*Pringle* 3335); *f*, *M. pubescens* (*Arsène*); g, *M. longiligula* (*Reeder & Reeder* 2699); *h*, *M. rigens* (*Blumer* 1491). Drawings are diagrammatic and not drawn to scale.

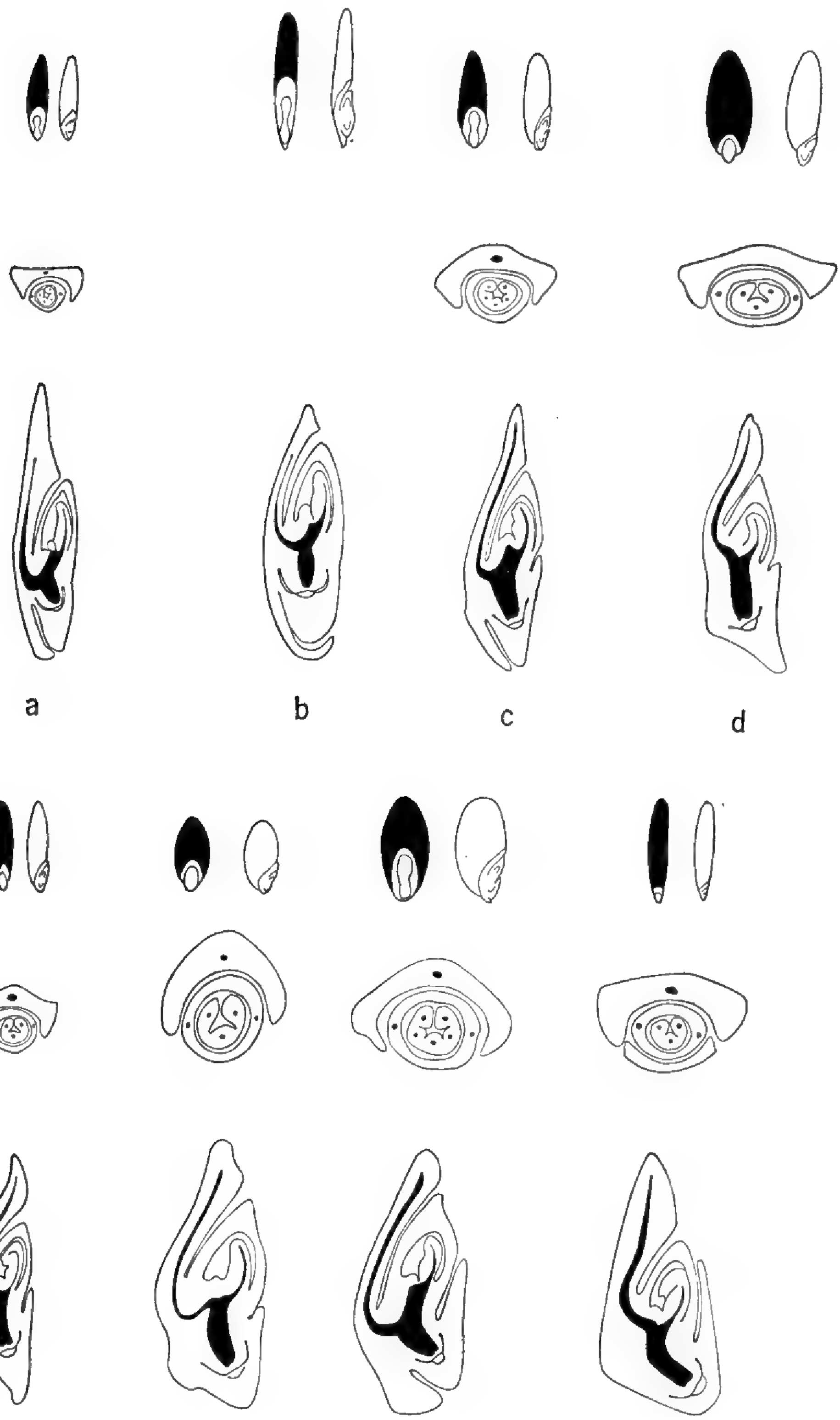

FIGURE 3.—Outline drawings of caryopses, median sagittal sections, and transverse sections through the coleoptile region of embryos of *Muhlenbergia* and other genera: *a, Muhlenbergia macroura* (*Arsène*); *b, M. nigra* (*Cook*); *c, M. schreberi* (no voucher); *d, Agrostis scabra* (*Goodding*); *e, Cinna arundinacea* (*Tweedy*); *f, Polypogon monspeliensis* (*Hortus Botanicus Bruxellensis*); *g, Sporobolus wrightii* (*Goodding*); *h, Stipa avenacea* (*Reeder & Reeder* 233). Drawings are diagrammatic and not drawn to scale.

The caryopses and embryos of *Muhlenbergia* species of the Epicampes group have the following features:

Caryopsis: The embryo is relatively large in comparison with the endosperm.

Embryo: Median sagittal section.

1. A distinct internode is present in the vascular system between the point of divergence of the trace to the scutellum and the trace to the embryonic leaves (P).
2. An epiblast is present (+).
3. A cleft is present between the lower part of the scutellum and the coleorhiza (P).

Embryo: Transverse section.

4. The margins of the embryonic leaf contain few bundles and the margins do not overlap (F).

The embryo formula (see Reeder, 1957) for these species is P+PF, the chloridoid-eragrostoid type: *Muhlenbergia* and *Sporobolus* also are chloridoid-eragrostoid, but *Agrostis*, *Cinna*, *Polypogon*, and *Stipa* are festucoid.

Muhlenbergia macroura and *M. nigra* differ from the other species in lacking an epiblast, unusual for chloridoid-eragrostoid species. On the basis of gross morphology and leaf anatomy, however, they are quite similar to *M. rigens* and an epiblast is present in that species as well as in *M. dubioides*.

Of 12 caryopses examined from a single specimen of *Muhlenbergia pubescens* (*Soderstrom* 693), 7 had double embryos. However, other specimens of *M. pubescens* from different localities and all other species examined had single embryos.

Conclusions

The embryos of *Muhlenbergia* do not show basic differences characteristic of individual groups, except *M. macroura* and *M. nigra* which differ in the absence of an epiblast. As emphasized by Reeder, the embryo is most useful in indicating the placement of a grass within one of six natural groups of genera. The species of the Epicampes group are like other species of *Muhlenbergia* and *Sporobolus* and are related to grasses of the chloridoid-eragrostoid group. They do not show a relationship to *Agrostis* and other festucoid genera of the Agrostideae with which they have been traditionally associated. A summary of embryo characters follows (see also figs. 2 and 3):

Genus and/or species	*Embryo/ endosperm large (P) small (F)*	*Internode in trace present (P) absent (F)*	*Epiblast present (+) absent (−)*	*Cleft in scutellum present (P) absent (F)*	*Embryonic leaf margins meet, bundles few (F) margins overlap, bundles many (P)*	*Formula*
Muhlenbergia						
Gigantea type of leaf anatomy						
M. emersleyi	P	P	+	P	F	P+PF
M. gigantea	P	P	+	P	F	P+PF
M. grandis	P	P	+	P	F	P+PF
M. longiligula	P	P	+	P	F	P+PF
M. macrotis	P	P	+	P	F	P+PF
M. pubescens	P	P	+	P	F	P+PF
M. robusta	P	P	+	P	F	P+PF
Rigens type of leaf anatomy						
M. macroura	P	P	−	P	F	P−PF
M. nigra	P	P	−	P	(Not seen)	P−P
M. rigens	P	P	+	P	F	P+PF
Type species						
M. schreberi	P	P	+	P	F	P+PF
Agrostis	F	F	+	F	F	F+FF
Cinna	F	F	+	F	F	F+FF
Polypogon	F	F	+	F	F	F+FF
Sporobolus	P	P	+	P	F	P+PF
Stipa	F	F	+	F	F	F+FF

Lodicules

Lodicules are small hyaline or fleshy scalelike structures subsessile between the lemma and palea of a grass floret. At time of anthesis when they reach their maximum development they become swollen and force the lemma and palea apart, thereby allowing the stamens to become exserted from the spikelet. They are thought to represent a reduced inner whorl of perianth parts, the outer whorl having been lost completely through evolution. Although only two lodicules are found in most genera, three are present in the floret of *Stipa* and most bamboos; lodicules are lacking entirely in *Anthoxanthum*, *Cenchrus*, and *Pennisetum*. The lodicules are usually separate, but are fused in *Melica* and *Glyceria*. Not only are differences in lodicules among genera found with respect to the number present, but also in size and shape, manner of thickening, and vascularization.

Zuderell (1909) examined the lodicule anatomy of about 50 species of grasses and in the same year Krause mentioned that lodicules might be of systematic value. Apparently, not until recently has real emphasis been placed on these structures as indicators of natural

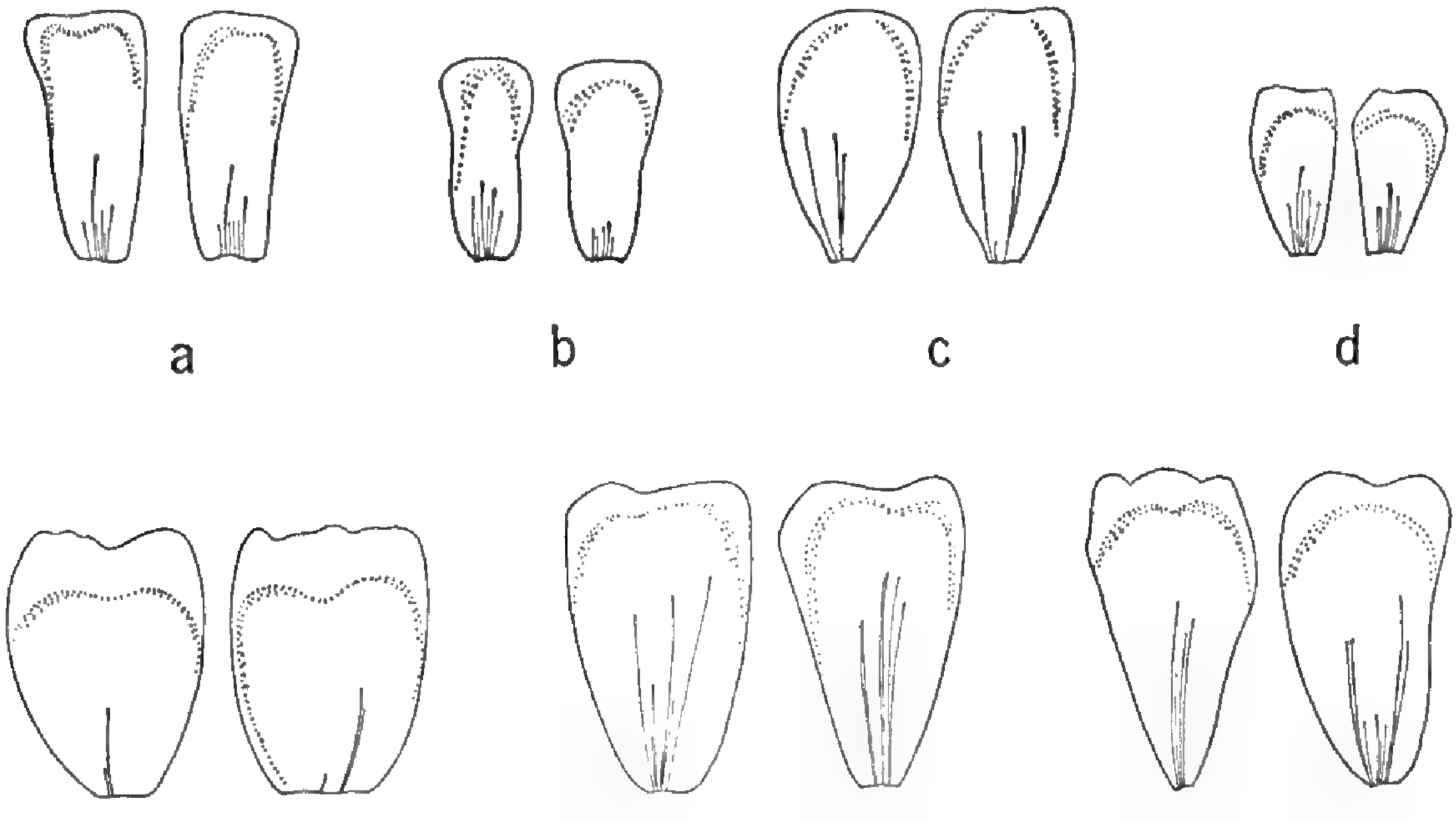

FIGURE 4.—Lodicules of Muhlenbergias in the *Podosemum* section, all times 46: *a*, *M. angustata* (*Camp* E–2519); *b*, *M. glabrata* (*Amer. Gr. Nat. Herb.* 1356); *c*, *M. dubia* (*Soderstrom* 509); *d*, *M. rigida* (*Soderstrom* 640); *e*, *M. macroura* (*Soderstrom* 551); *f*, *M. nigra* (*Pringle* 11739); g, *M. palmeri* (*Pringle* 1417).

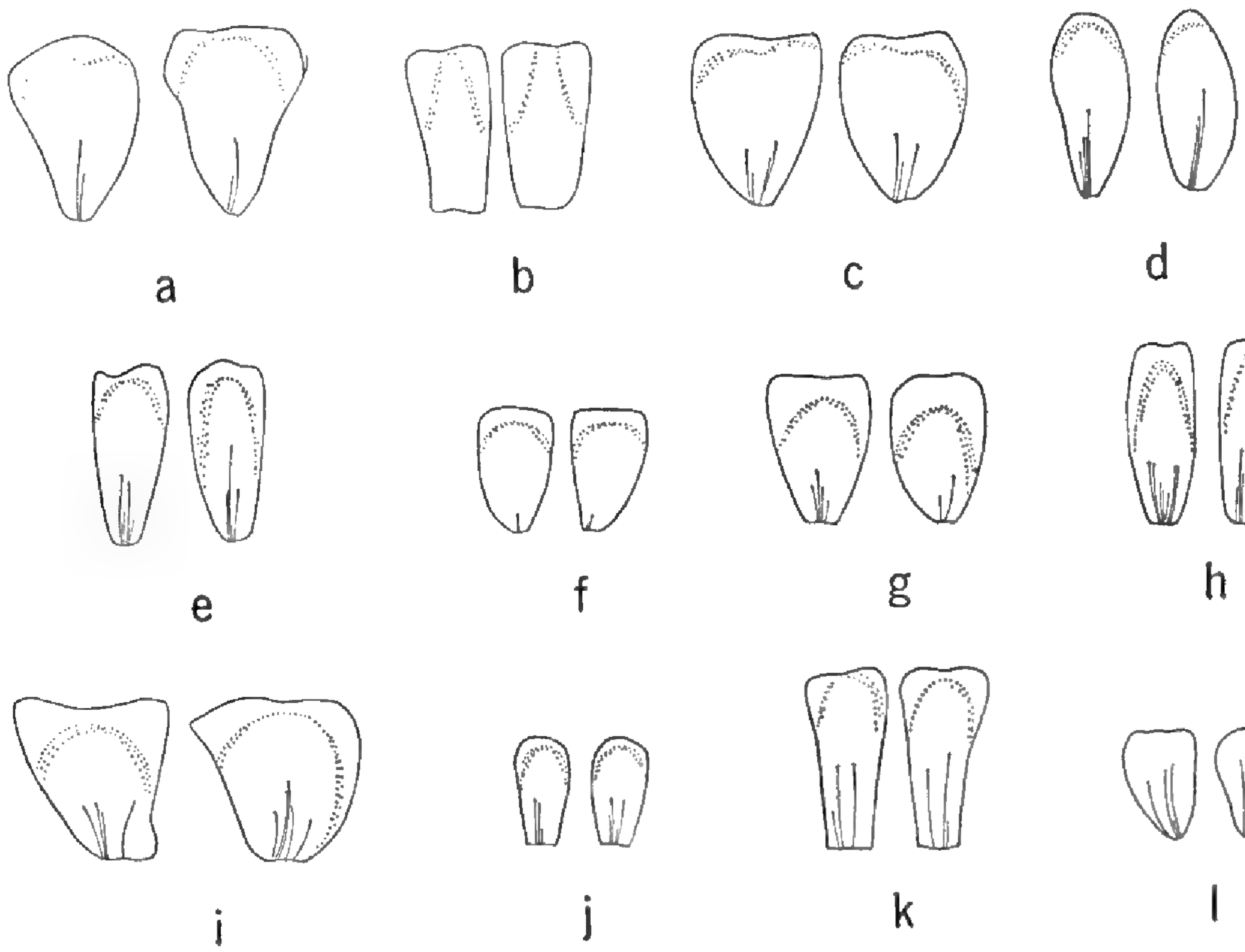

FIGURE 5.—Lodicules of Muhlenbergias in the *Podosemum* and *Epicampes* sections, all times 45: *a*, *M. firma* (*Amer. Gr. Nat. Herb.* 1351); *b*, *M. rigens* (*Soderstrom* 731); *c*, *M. capillaris* (*Kral & Godfrey* 54211); *d*, *M. xerophila* (*Goodding* A–9493); *e*, *M. expansa* (*Godfrey* 8151); *f*, *M. arenicola* (*Pringle* 479); *g*, *M. articulata* (*Pringle* 3913); *h*, *M. reverchonii* (*Silveus* 2478); *i*, *M. longiglumis* (*Pringle* 2365); *j*, *M. stricta* (*Soderstrom* 642); *k*, *M. involuta* (*Silveus* 780); *l*, *M. emersleyi* (*Soderstrom* 746).

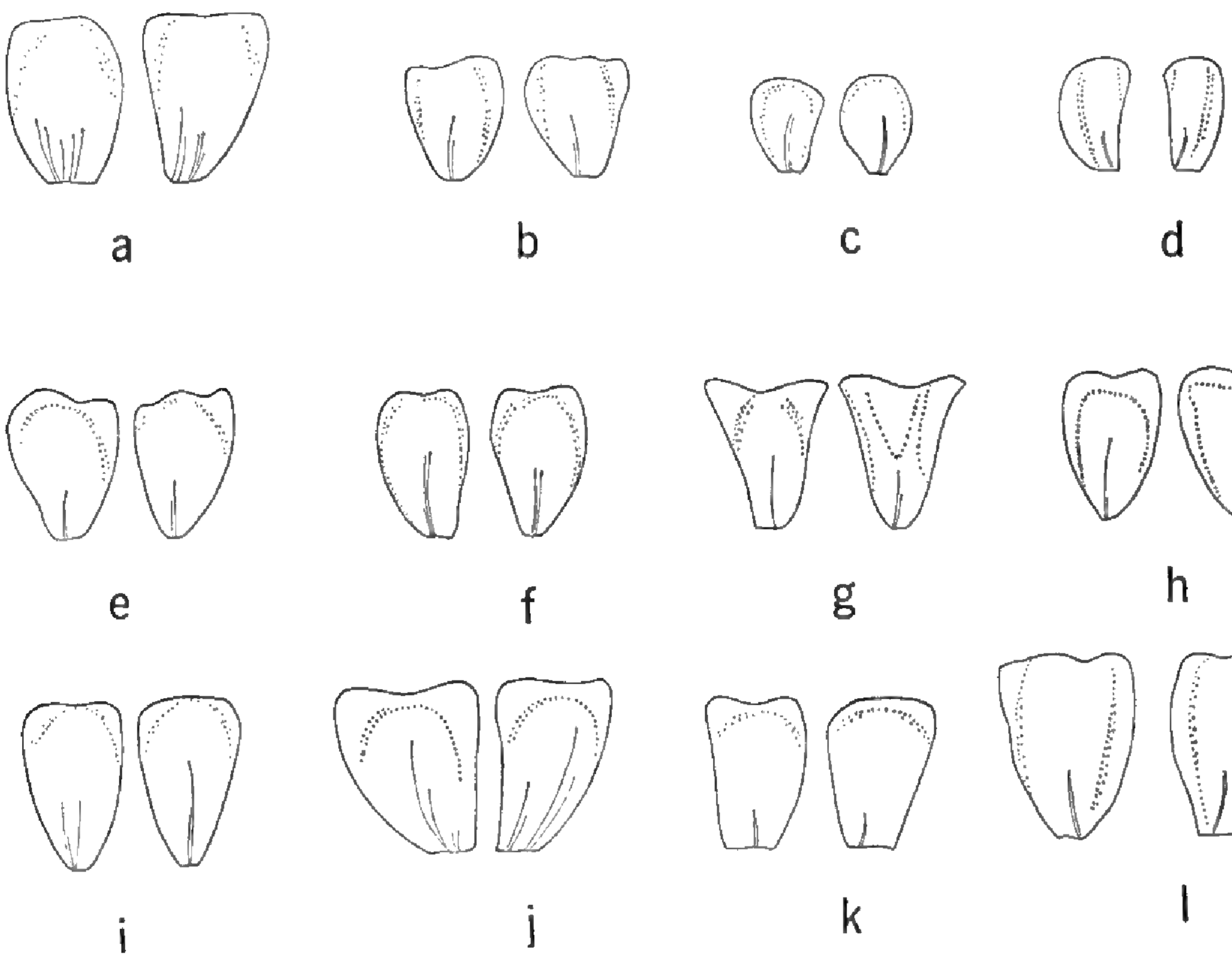

FIGURE 6.—Lodicules of Muhlenbergias in the *Epicampes* section, all times 46: *a*, *M. distans* (*Pringle* 5374); *b*, *M. speciosa* (*Reeder & Reeder* 2476); *c*, *M. grandis* (*Pringle* 2765); *d*, *M. distichophylla* (*Pringle* 2346); *e*, *M. robusta* (*Arsène*); *f*, *M. versicolor* (*Smith* 927); *g*, *M. macrotis* (*Mexia* 9098); *h*, *M. pubescens* (*Soderstrom* 483); *i*, *M. lindheimeri* (*Burr* 513); *j*, *M. robusta* (*Soderstrom* 382); *k*, *M. longiligula* (*Reeder & Reeder* 3222); *l*, *M. gigantea* (*Reeder & Reeder* 2488).

relationships. Stebbins (1956), in a study of intergeneric hybrids of *Lolium* and *Festuca*, pointed out that cytological findings agree with those based on studies of the grass flower and caryopsis. He illustrated four types of lodicules which he designated panicoid, chloridoid, festucoid, and bambusoid. In the panicoid and chloridoid types the lodicules are truncate at the apex, but pointed in the festucoid and bambusoid types. Church (1949) also mentioned the value of using characters of the grass flower, including lodicules, in systematics. Although Hubbard (1934, 1959 rev.) figured the lodicules of many species, he did not discuss them from a comparative viewpoint. Some understanding of the diversity of structure among genera can be gained from his sketches of the lodicules of nearly every species of grass from the British Isles (1954). Bor (1960) likewise included sketches of the lodicules of many grasses.

Reeder and Ellington (1960) demonstrated that the genus *Calamovilfa* is chloridoid and should be removed from the Agrostideae. Their conclusions were based on lodicule anatomy along with embryo structure, leaf anatomy and epidermis, and chromosome size and number. Tateoka (1960a) also used lodicules, among other floral

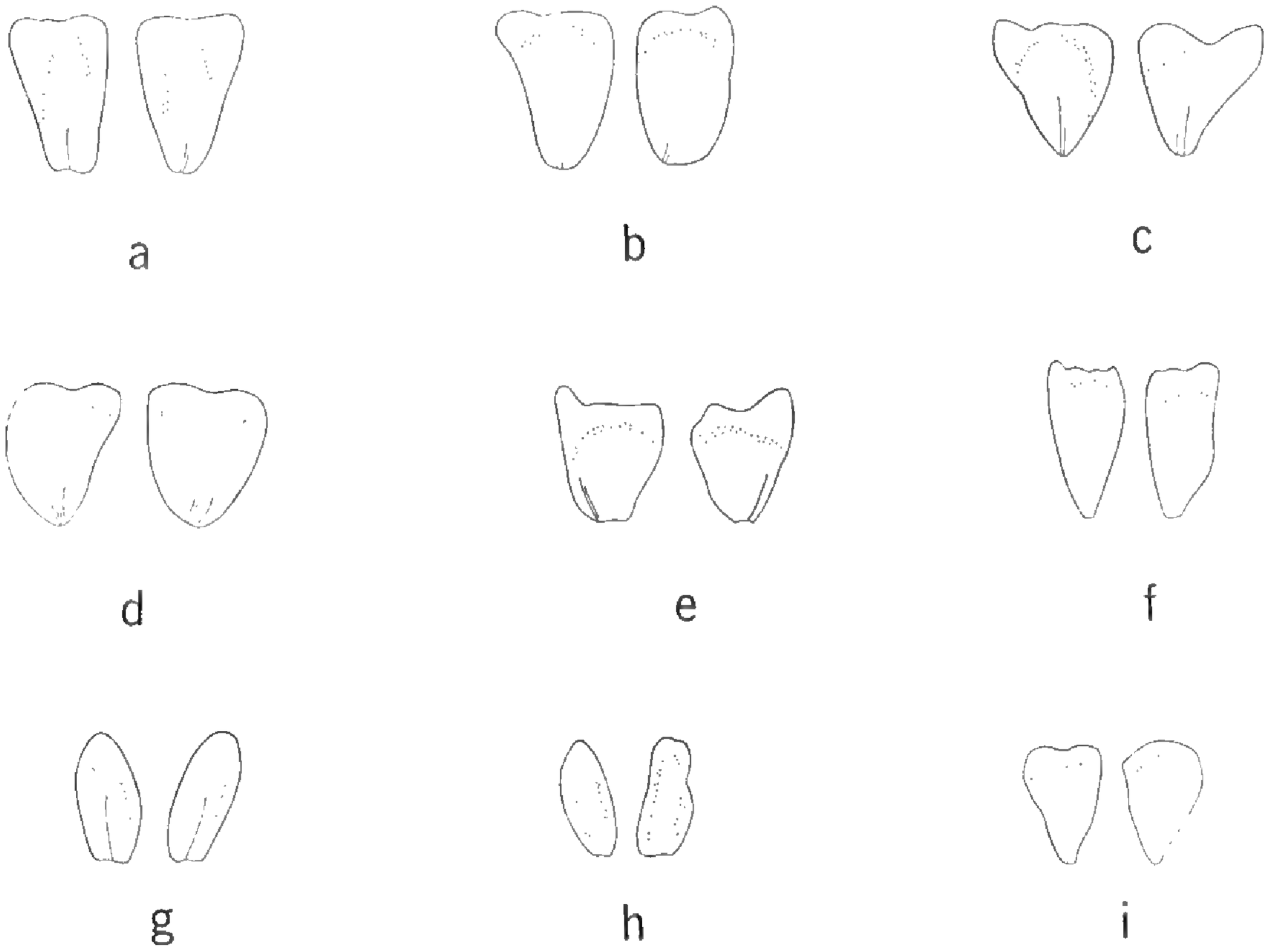

FIGURE 7.—Lodicules of Muhlenbergias other than the *Podosemum* or *Epicampes* sections, all times 50: *a*, *M. quadridentata* (*Hinton* 4389); *b*, *M. montana* (*Arsène* 5811); *c*, *M. schreberi* (no voucher); *d*, *M. wrightii* (*Goodding & Hardies* A–8498); *e*, *M. uniflora* (*Miller* 130); *f*, *M. biloba* (*Pringle* 819); *g*, *M. depauperata* (*Reeder & Reeder* 2279); *h*, *M. brevis* (*Reeder & Reeder* 2620); *i*, *M. torreyi* (*Goodding* M–189).

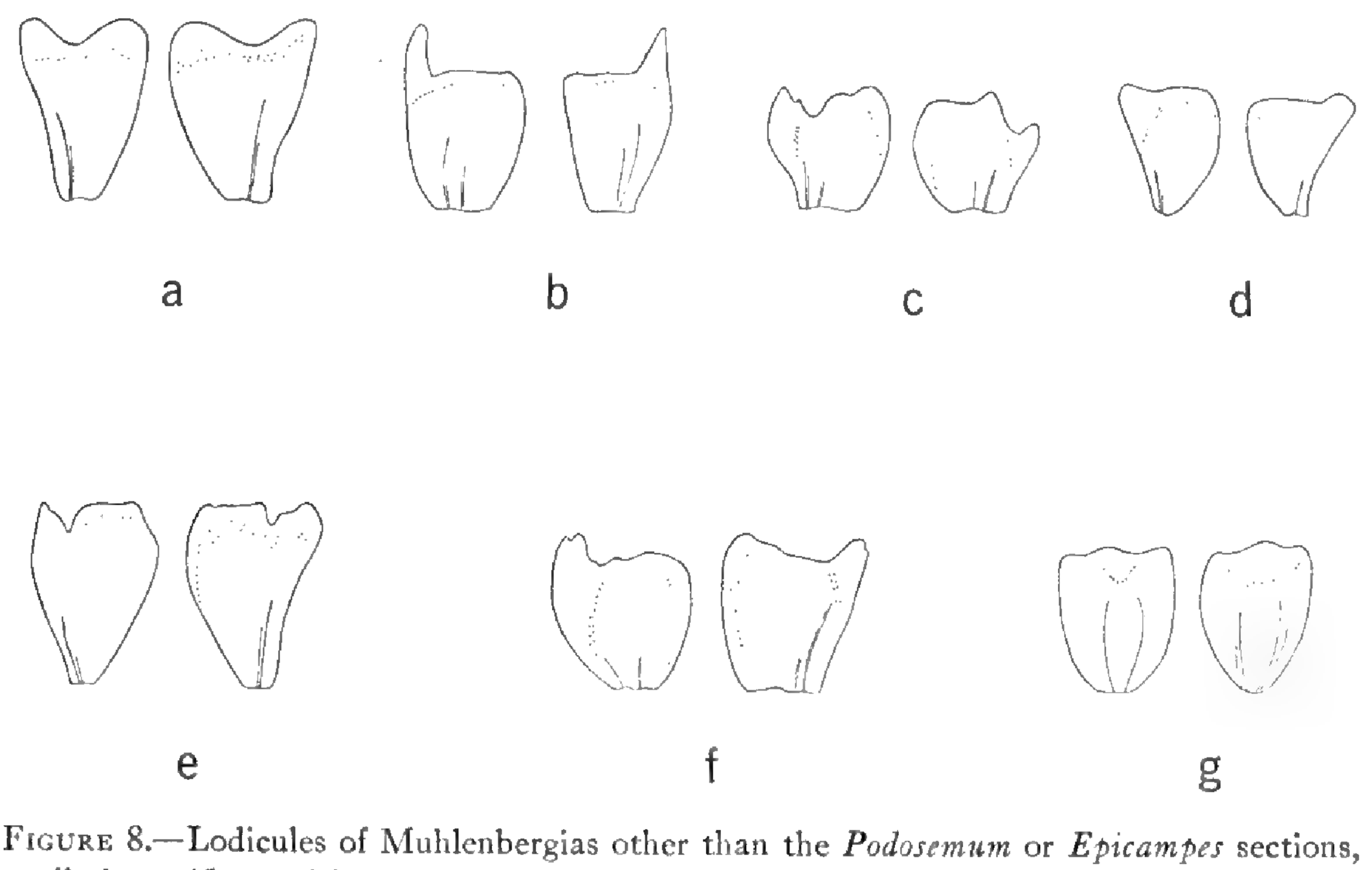

FIGURE 8.—Lodicules of Muhlenbergias other than the *Podosemum* or *Epicampes* sections, all times 45: *a*, *M. sylvatica* (no voucher); *b*, *M. racemosa* (*Cornman*); *c*, *M. frondosa* (no voucher); *d*, *M. andina* (*Reeder & Reeder* 1808); *e*, *M. glomerata* (*Reeder & Reeder* 944); *f*, *M. mexicana* forma *ambigua* (no voucher); *g*, *M. torreyana* (*Bissell*).

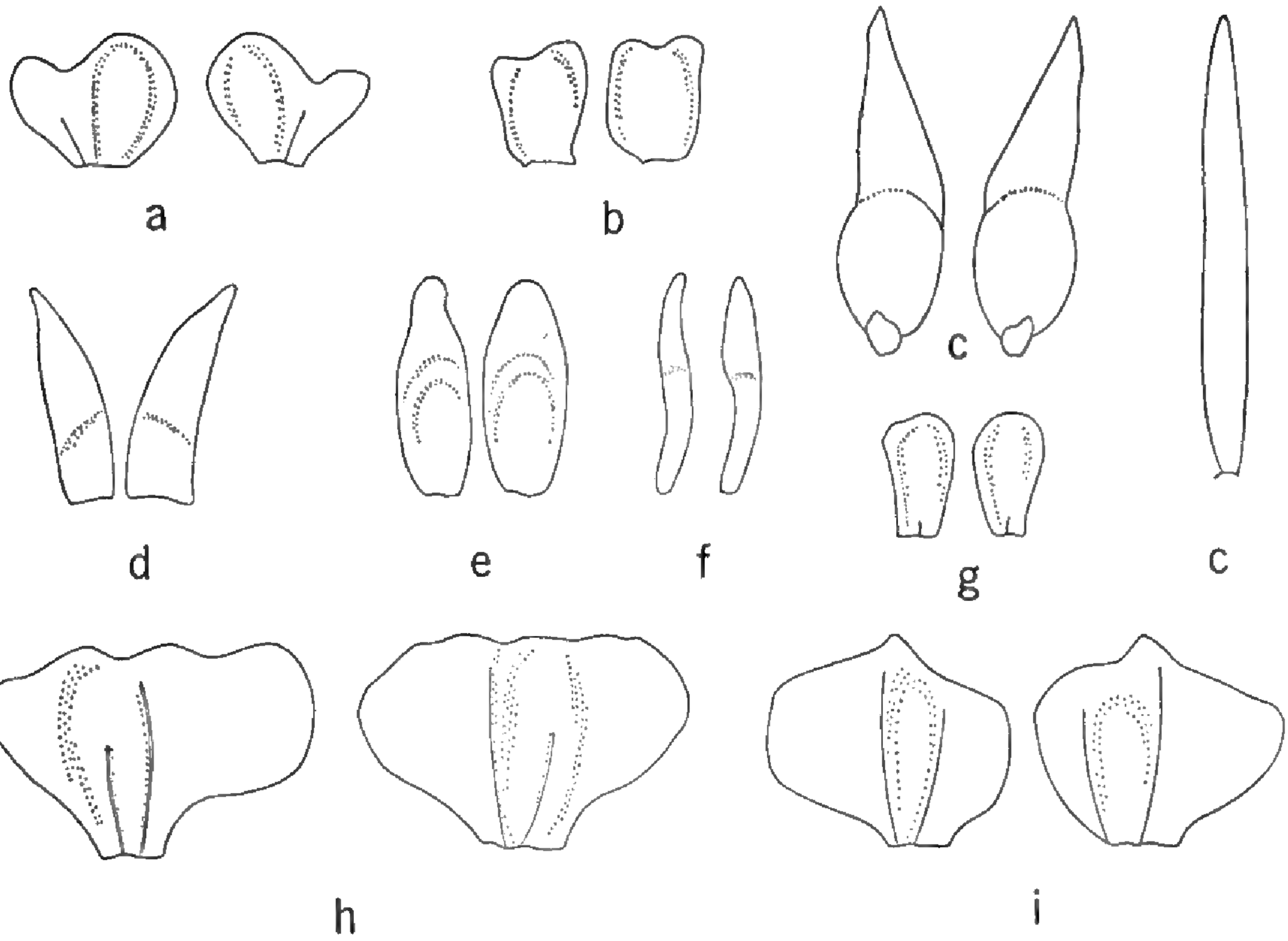

FIGURE 9.—Lodicules of genera that have been associated with *Epicampes*, all times 44: *a*, *Sporobolus wrightii* (*Toumey*); *b*, *Blepharoneuron tricholepis* (*Reeder & Reeder* 1807); *c*, *Stipa avenacea* (*Reeder & Reeder* 233); *d*, *Agrostis alba* (*Dudley*); *e*, *Cinna arundinacea* (no voucher); *f*, *Polypogon monspeliensis* (*Swan*); *g*, *Lycurus phleoides* (*Reeder & Reeder* 2352); *h*, *Sporobolus asper* (*Nichols*); *i*, *Sporobolus heterolepis* (*Nichols*).

features, to show the relationships of several genera of the Festuceae. Reeder [10] reported on the preliminary results of his study of the lodicules of over 300 species, representing 230 genera. Decker (1964), in a study of 135 genera, utilized information from the lodicules, along with other microcharacters, to determine the naturalness of the classical tribe Festuceae. Hsu's (1963) study is an example of lodicules figured for several species in a single genus.

In the present study the lodicules of 47 species of *Muhlenbergia* (including *Epicampes*) have been examined. Included are 13 species with a Gigantea type of leaf anatomy, 15 with a Rigens type, 3 intermediate between the two, the type species of *Muhlenbergia*, and 15 additional species. Line drawings of the lodicules of each of these species, in addition to those of several other genera with which *Epicampes* has been associated, appear in figures 4–9. The vascular tissue of the lodicules and manner of thickening are indicated in these drawings.

All lodicules were selected from spikelets of herbarium specimens in which the anthers were fully developed but not yet exserted.

[10] Paper read at meetings of the American Institute of Biological Sciences, Stillwater, Oklahoma, 1960.

The spikelets were boiled in water for several minutes, transferred to a watch glass, and the lodicules dissected out under the low power of a binocular microscope. The shape of the lodicules was drawn at this time and the areas of thickening noted, then the lodicules were mounted in glycerine jelly without staining. From 2 to 3 weeks later the excess glycerine jelly was removed and the slides ringed with diaphane. The vascularization was drawn later from the slides under the high power of a compound microscope.

Most of the species of *Muhlenbergia* examined possess lodicules more or less rectangular in outline. The thickened portion of the lodicules extends from the base to near the apex; the upper margins are of a thinner texture. One to many vascular traces usually are present in the form of annular tracheids—rarely are they lacking entirely. According to Stebbins (1956) and Reeder and Ellington (1960), these lodicules are of the chloridoid type.

The lodicules of species with a Gigantea type of leaf anatomy (figs. 5*l* and 6*a–j, l*) possess one to four or five vascular traces. Apart from small differences in size and amount of vascularization, the lodicules appear to be rather similar. Lodicules of the species with a Rigens type of anatomy (figs. 4*a–g* and 5*a–h*) usually possess two to many traces. The lodicules of *M. rigens* (fig. 5*b*) are atypical in having no vascular traces; in *M. arenicola* (fig. 5*f*) the one or two traces present are almost negligible. The considerable difference in lodicule size is attributable to the difference in the size of the spikelets. The large lodicules of *M. macroura* (fig. 4*e*), *M. nigra* (fig. 4*f*), and *M. palmeri* (fig. 4*g*) reflect the large spikelet size in these species. Lodicule shape, degree of thickening, and vascularization, with little exception, are similar in all species with a Rigens type of leaf anatomy.

Species of *Muhlenbergia* not of the Rigens or Gigantea groups exhibit the same kind of thickening in the lodicules and in degrees of vascularization. The lodicules of many of them are like the species with a Rigens or Gigantea type of anatomy—*M. torreyana* (fig. 8*g*), *M. quadridentata* (fig. 7*a*), *M. montana* (fig. 7*b*), and *M. wrightii* (fig. 7*d*).

In the type species of *Muhlenbergia*, *M. schreberi* (fig. 7*c*), the upper margin of the lodicule is extended on one side into a small "wing." A similar lodicule is found in *M. uniflora* (fig. 7*e*). In *M. racemosa* (fig. 8*b*), a species with scaly rhizomes, the upper corners of the lodicules are prominently projected. Other species with scaly rhizomes also have winglike extensions, to a lesser or greater degree—*M. sylvatica* (fig. 8*a*), *M. frondosa* (fig. 8*c*), *M. andina* (fig. 8*d*), *M. glomerata* (fig. 8*e*), and *M. mexicana* forma *ambigua* (fig. 8*f*).

Interesting differences are found among lodicules of various genera that, in one system of classification or another, have been considered

as closely related to the Epicampes group. Of the festucoid type *Agrostis* (fig. 9*d*), *Cinna* (fig. 9*e*), *Polypogon* (fig. 9*f*), and *Stipa* (fig. 9*c*) have long narrow lodicules with only the lower part thickened. *Stipa* further differs in having three, rather than two, lodicules. *Blepharoneuron* (fig. 9*b*) possesses truncate lodicules in which the thickening extends from the base to the apex, and is thus of the chloridoid type, as are the lodicules of *Lycurus* (fig. 9*g*) and *Sporobolus* (figs. 9*a,h,i*). *Blepharoneuron* and *Lycurus* show no fundamental differences from *Muhlenbergia*. However, the lateral unthickened margins in *Sporobolus* are considerably wider than in any of the species of *Muhlenbergia* examined.

Conclusions

On the basis of lodicules, the species of *Muhlenbergia*, including *Epicampes*, are of the chloridoid type, along with such genera as *Blepharoneuron*, *Lycurus*, and *Sporobolus*. They are unlike the festucoid genera *Agrostis*, *Cinna*, *Polypogon*, and *Stipa*.

Differences of lodicules among the species of *Muhlenbergia* are of comparatively little value in recognizing groups of related species. However, the type species of *Muhlenbergia* and similar species with scaly rhizomes do exhibit a difference in the shape of the lodicules, and further studies on the remaining species of this genus may reveal that other species have distinctive lodicules.

A summary of the lodicule characters for each of the genera discussed follows (see also figs. 4–9):

Genus	*Lodicules per floret*	*Shape*	*Thickening*	*Vascularization*	*Lodicule group*
Muhlenbergia Gigantea type of leaf anatomy	2	truncate	thickened from base to near apex; lateral margins thin	1–many traces	C *
Rigens type of leaf anatomy	2	truncate	thickened from base to near apex; lateral margins thin	1–many traces	C
Type species, *M. schreberi* and allies	2	truncate, with projections	thickened from base to near apex, lateral margins thin	2–4 traces	C

*See footnote at end of table.

Genus	*Lodicules per floret*	*Shape*	*Thickening*	*Vascularization*	*Lodicule group*
Agrostis	2	narrow, pointed	thickened below; thin above	lacking	F
Blepharoneuron	2	truncate	thickened from base to apex, lateral margins thin	lacking	C
Cinna	2	narrow, rounded	lower ¾ thickened, upper ¼ thin	lacking	F
Lycurus	2	truncate	thickened from base to near apex; lateral margins thin	1 short trace	C
Polypogon	2	narrow, pointed	lower ½ thickened, upper ½ thin	lacking	F
Sporobolus	2	very wide, more or less truncate	thickened from base to near apex; lateral margins thin	1–several traces	C
Stipa	3	narrow, pointed	thickened below, thin above	lacking	F

C=chloridoid. F=festucoid.

Chromosomes

Avdulov (1931) was the first worker to utilize cytological information as a basis for a new system of classification of the Gramineae. Subsequent workers, Prat (1936), Pilger (1954), and Stebbins (1956), have also employed cytological in addition to other data in their proposed systems. The role of cytology in grass systematics has been thoroughly reviewed by Tateoka (1960b).

Although cytological studies were not undertaken in the present investigation, several workers have published results of studies on many species of *Muhlenbergia* (including *Epicampes*) and putative allied genera, from which the following summary was made.

According to Darlington and Wylie (1956) x=7 is the basic chromosome number for *Agrostis*, *Cinna*, and *Polypogon*. These genera traditionally have been placed with *Epicampes* in the tribe Agrostideae, along with *Stipa*, *Sporobolus*, and *Muhlenbergia*. On the basis of cytology, *Agrostis*, *Cinna*, and *Polypogon* are festucoid, in corrobo-

ration with the conclusions based on other studies. The basic numbers Darlington and Wylie listed for *Stipa* are x=9, 10, 11, 12, 14, 16, or 17; for *Sporobolus*, x=9, 10, or 12; and for *Muhlenbergia*, x=9, 10, or 21. A survey of the chromosome numbers published for *Sporobolus* indicates that most of the species have a basic number of 9 chromosomes, whereas most of the species of *Muhlenbergia* (including *Epicampes*) have a basic number of x=10. *Stipa*, in which a high degree of aneuploidy occurs (Stebbins & Love, 1941, p. 379), does not appear to have a consistent basic number. Stebbins (1956) considers this genus to be a member of a specialized line, the Stipeae, the members being neither completely festucoid nor panicoid. He lists x=11 or 12 as the basic number for this group.

Chromosome counts of seven species of the Epicampes group of *Muhlenbergia* are listed below: *M. emersleyi* (2n=40 & 60); *M. gigantea* (2n=20); *M. lindheimeri* (2n=20); *M. macroura* (2n=40); *M. pubescens* (2n=40); *M. rigens* (2n=40); and *M. reederorum* (2n=68). Following is a list of American species of *Muhlenbergia* for which chromosome numbers have been determined:

Species of Muhlenbergia	*2n*	*Authority*
Gigantea type of leaf anatomy		
M. emersleyi	40	Brown (1950)
	60	Reeder (1961, unpublished)
M. gigantea	20	Tateoka (1962)
M. lindheimeri	20	Brown (1950)
	20	Reeder (1965, unpublished)
M. pubescens	40	Reeder (1961, unpublished)
M. reederorum	68	Reeder (1965, unpublished)
Rigens type of leaf anatomy		
M. macroura	40	Tateoka (1962)
M. reverchonii Vasey & Scribn.	40	Brown (1951)
M. rigens	40	Stebbins & Love (1941)
	40	Reeder (1961, unpublished)
M. rigida (H.B.K.) Trin.	40	Gould (1958)
Other species		
M. andina (Nutt.) Hitchc.	20	Myers (1947; counted by Stebbins)
M. asperifolia (Nees & Mey.) Parodi	20	Myers (1947; counted by Stebbins)
M. brachyphylla Bush	40	Brown (1950)
M. filiformis (Thurb.) Rydb.	18	Myers (1947; counted by Stebbins)
M. mexicana Trin.	40	Avdulov (1931)
M. monticola Buckl.	40	Brown (1951)
M. polycaulis Scribn.	20	Brown (1951)
M. porteri Scribn.	20	Brown (1951)
	40	Gould (1960)
M. pungens Thurb. in A. Gray	42	Nielsen & Humphrey (1937)
	60	Nielsen (1939)

Species of Muhlenbergia	*2n*	*Authority*
M. racemosa (Michx.) B.S.P.	40	Avdulov (1931)
M. repens (Presl) Hitchc.	60	Brown (1951)
M. richardsonis (Trin.) Rydb.	40	Stebbins & Love (1941)
M. schreberi Gmel.	40	Gould (1958)
M. squarrosa (Trin.) Rydb.	40	Bowden (1960)
	40	Stebbins & Love (1941)
M. sylvatica (Torr.) Torr. ex Gray	40	Avdulov (1931)
M. tenuifolia (H.B.K.) Kunth	40	Tateoka (1962)
M. uniflora (Muhl.) Fern.	ca. 42	Bowden (1960)

On the basis of cytology, *Muhlenbergia* (including the Epicampes group) is panicoid (or chloridoid) rather than festucoid, as the chromosomes are small and in multiples of 10. The chloridoid genus *Sporobolus* has a basic number of 9 and thus is distinct from *Muhlenbergia.* Of the few species known cytologically, the diploid species of the Epicampes group, *M. lindheimeri* and *M. gigantea,* are quite uniform morphologically as would be expected. Two counts are available for the *M. emersleyi* complex, one a tetraploid and the other a hexaploid; further counts will probably reveal a range of numbers among the various forms assigned to the species. The most interesting count is of *M. reederorum,* evidently an aneuploid. From the gross morphology *M. reederorum* appears to have been derived in part from *M. longiligula,* but we have no count for that species.

In regard to the disposition of *Epicampes* itself, Stebbins & Love (1941, p. 379) said:

> The chromosome number and size obtained for *Muhlenbergia richardsonis* (Trin.) Rydb. and *M. rigens* (Benth.) Hitchc. (2n=40, fig. 22) agrees with that reported by Avdulov (1931) for other species of *Muhlenbergia.* Since the chromosomes of *M. rigens* are closely similar to those of the other species of the genus, the union by Hitchcock of the genera *Epicampes* and *Muhlenbergia* is well supported by the cytological evidence.

The Disposition of *Epicampes*

The results of studies of the leaf anatomy and epidermis, embryos, lodicules, and chromosomes agree that the species traditionally regarded as *Epicampes* are of the chloridoid alliance. Several genera of the tribe Agrostideae, *Agrostis, Cinna,* and *Polypogon,* are of the festucoid alliance and are not closely related to *Epicampes* as has often been suggested.

Features of the embryos have been useful only in demonstrating that the species of the Epicampes group are chloridoid but did not serve to differentiate genera within this alliance. The lodicules of the Epicampes group are also of the chloridoid type as are those of *Muhlenbergia* but no fundamental differences were found among

them. The lodicules of *Sporobolus* were found to be somewhat distinctive in being larger and wider than those of *Muhlenbergia* (including *Epicampes*). In the few species of the Epicampes group with a known chromosome number, the basic number is the same as that of other species of *Muhlenbergia*, but differs from that of *Sporobolus*. This cytological information should indicate that species of the Epicampes group are more closely related to *Muhlenbergia* than to *Sporobolus*.

The studies most useful in clarifying the relationships of the Epicampes group have been those of leaf anatomy and, to a more limited extent, the leaf epidermis. They have shown that the Epicampes group is chloridoid and have pointed to the most closely related species within *Muhlenbergia*.

The species of *Muhlenbergia*, including the Epicampes group, possessing a Rigens or Gigantea type of leaf anatomy have the following morphological features in common (all species examined with other types of leaf anatomy also differ morphologically in one or more respects from these):

1. Plants perennial, strongly caespitose (rhizomes never produced).
2. Culms stout, robust, erect, not branching or rooting at the nodes.
3. First and second glumes nerveless or 1-nerved.

This group is well defined not only on the basis of gross morphology but also in characters of leaf anatomy and epidermis; on this evidence I feel this group of species should be treated as a subgenus of *Muhlenbergia* comprising two sections. The section *Epicampes*, characterized by a Gigantea type of leaf anatomy, includes among others *M. robusta* (including *E. strictus*, the type of the genus *Epicampes*). The section *Podosemum*, characterized by a Rigens type of leaf anatomy, includes among others *M. rigens*, *M. macroura*, and *M. capillaris* (based on *P. capillare*, the type species of the genus *Podosemum*).

Systematic Treatment

Muhlenbergia

Muhlenbergia Schreb. *in* L. Gen. Pl., ed. 8, 55. 1789.

Type species: *Muhlenbergia schreberi* Gmel. *in* L., Syst. Nat., ed. 13, 2:171. 1791.

Subgenus 1. *Muhlenbergia.*

Subgenus 2. *Podosemum* (Desv.) Soderstrom, stat. nov.

Podosemum Desv., Nouv. Bull. Soc. Philom. Paris 2:188. 1810.

Type species: *Podosemum capillare* (Lam.) Desv.=*Muhlenbergia capillaris* (Lam.) Trin. Originally described as *Stipa capillaris* Lam. Tabl. Encycl. 1:158. 1791.

Morphological Features: Plants perennial, caespitose, rhizomes not produced; culms rather stout to robust, erect, not branching or rooting at the nodes; glumes nerveless or 1-nerved (rarely an additional faint nerve or nerves present).

Anatomical Features of the Leaf: Phloem of the 1° vascular bundles sclerosed; large caps of sclerenchyma present in the 1° units.

Section 1. *Podosemum*[11]

Morphological Features: Basal sheaths rounded; ligule firm; glumes equal or unequal, shorter to longer than the floret, membranous to firm; awn of lemma (when present) arising terminally or dorsally, from just below the tip.

Anatomical Features of the Leaf: Central 1° unit not differentiated from other 1° units; no keel present; 3° units often present in addition to 1° and 2° units, the units alternating in a like fashion throughout the leaf.

Species Included (asterisked species originally described as *Epicampes*): *M. angustata, M. arenicola, M. articulata, M. capillaris, M. dubia, M. dubioides, M. elongata, M. expansa, M. firma, M. glabrata, M. holwayorum, M. lucida, M. macroura, M. nigra, M. palmeri, M. reverchonii, *M. rigens, M. rigida, M. xerophila.*

Section 2. *Epicampes* (J. S. Presl) Soderstrom, stat. nov.

Basionym: *Epicampes* J. S. Presl *in* K. B. Presl, Rel. Haenk. 1:235. *t. 39.* 1830. Type species: *Epicampes strictus* Presl, loc. cit. =*M. robusta* (Fourn.) Hitchc.

Morphological Features: Basal sheaths compressed-keeled; ligule membranous throughout (firmer below, membranous above in a few); glumes about equal, generally longer than the floret, membranous, nerveless or indistinctly 1-nerved; awn of lemma (when present) arising from a mucronate tip or dorsally, from just below the tip.

Anatomical Features of the Leaf: Central 1° unit with a large basal cap of sclerenchyma—this and adjacent units sunken in a confluent mass of thick-walled parenchyma, forming a keel; only 1° and 2° units present, these alternating in a like pattern on either side of the keel.

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[11] Since this section includes the type species of the next higher rank, the subgenus *Podosemum*, it appears without author citation. It does, however, coincide with Section 7 *Podosemum* (Desv.) Pilger *in* Die Natürlichen Pflanzenfamilien, 2nd ed., 14d:71. 1956, except for *Muhlenbergia distichophylla* (Presl) Kunth which, under the present treatment, belongs in section 2, *Epicampes*. Section 4 *Cinnastrum*, of Pilger's work (p. 69), also belongs in section *Podosemum* of my treatment.

SPECIES INCLUDED (asterisked species originally described as *Epicampes*): *M. aurea, M. breviligula, M. distans, M. distichophylla, *M. emersleyi, *M. gigantea, M. gooddingii, *M. grandis, M. inaequalis, M. iridifolia, M. lehmanniana, *M. lindheimeri, M. longiglumis, *M. macrotis, *M. mutica, M. pubescens, M. pubigluma, *M. robusta, M. scoparia, M. speciosa, M. versicolor, *M. virletii, M. xanthodas.*

Species Intermediate Between *Epicampes* and *Podosemum*

*M. involuta, *M. longiligula, M. reederorum, M. stricta.*

Key to the major groups of *Muhlenbergia*

Phloem of the primary vascular bundles partially sclerosed; strongly caespitose perennials; culms erect, simple, usually stout and robust; glumes nerveless or 1-nerved . . . . . Subgenus **Podosemum**

Basal sheaths rounded; ligule firm (coriaceous); glumes equal or unequal, shorter to longer than the floret . . . . . Section 1. **Podosemum**

Basal sheaths compressed-keeled; ligule membranous (sometimes firm below); glumes about equal, generally longer than the floret . Section 2. **Epicampes**

Phloem of the primary vascular bundles not sclerosed; morphologically different in one or more of the above characters. . . . . Subgenus **Muhlenbergia**

Key to the species of Section *Epicampes*

(Including species intermediate between sections *Epicampes* and *Podosemum*)

Ligule broadly decurrent, firm and brown below, often membranous above; basal sheaths rounded, compressed, or compressed-keeled; old blades involute and somewhat arcuate.

Basal sheaths rounded or compressed, but not strongly keeled.

Lemmas long-awned, slightly pubescent on the margins toward the base (Arizona and Sonora, Mexico) . . . . . **1. M. gooddingii**

Lemmas awnless or with an awn no longer than 2 mm., glabrous.

Spikelets mostly 2.5–3 mm. long; blades 3–5.5 mm. wide, flat or inrolled; basal sheaths rounded (southwestern United States and northern Mexico) . . . . . **2. M. longiligula**

Spikelets mostly 3–4 mm. long; blades 1–2 mm. wide, involute; basal sheaths compressed and somewhat keeled.

Glumes equal to or longer than the floret; lemmas cuspidate or with an awn to 1 mm. long; spikelets averaging 4 mm. long (Mexico: Durango) . . . . . **3. M. reederorum**

Glumes shorter than the floret; lemmas with an awn 1–2 mm. long; spikelets averaging 3.5 mm. long (Texas) . . . . **4. M. involuta**

Basal sheaths strongly compressed-keeled.

Glumes and lemmas glabrous to scaberulous; culms glabrous to scaberulous below the nodes (Texas and Coahuila, Mexico) . . **5. M. lindheimeri**

Glumes and lemmas pubescent to lightly villous; culms pubescent below the nodes (Mexico: Coahuila and Nuevo León) . . . . **6. M. pubigluma**

Ligule not broadly decurrent, membranous (rarely somewhat firm below); basal sheaths strongly compressed-keeled; old blades flat or folded, not arcuate.

Sheath auricles present, long and pointed, often more than 1 cm. long.

Lemmas mostly glabrous.

Lemmas awnless or cuspidate, glabrous; spikelets mostly 2.5–3 mm. long; sheath auricles usually 1 cm. or more long (Mexico [Sinaloa to Oaxaca] and Guatemala) . . . . . **7. M. macrotis**

Lemmas long-awned, glabrous except for short hairs on the margins toward the base; spikelets mostly 2–2.5 mm. long; sheath auricles usually less than 1 cm. long (Mexico [Jalisco south] and Guatemala). **8. M. distichophylla**

Lemmas villous (Michoacán, Mexico, south to Honduras). **9. M. versicolor**

Sheath auricles lacking, or, if present, broad and rudimentary, not long and pointed.

Branches of the very large panicles widely spreading (tending to open after seed-set), long-naked below; lemmas completely glabrous; ligule usually about 1 cm. or more long.

Glumes equaling the floret, rounded or acutish; spikelets generally 1.5–2.2 mm. long (Mexico: Durango to Chiapas) . . . . . **10. M. gigantea**

Glumes several mm. longer than the floret, acute; spikelets generally 2.5–3 mm. long (Mexico: Veracruz and Chiapas) . . . . . **11. M. mutica**

Branches of the panicle ascending or appressed (usually opening outward at anthesis, tending to become appressed at seed-set), long-naked below or floriferous to base; lemmas with some pubescence (except usually *M. robusta*, this species with a short ligule unlike that of *M. gigantea* and *M. mutica*).

Glumes awn-tipped.

Lemma short-pilose over the lower half (Colombia and Venezuela). **12. M. inaequalis**

Lemma glabrous except for a tuft of short hairs at the base.

Spikelets 1–2 mm. long; glumes unequal; blades narrow, 2–3 mm.; ligule 8–16 mm. long, hyaline (Mexico: Chihuahua to Michoacán). **13. M. scoparia**

Spikelets about 4 mm. long; glumes about equal; blades wider, 4–7 mm.; ligule 5–7 mm. long, firm (Mexico: Jalisco). **14. M. iridifolia**

Glumes muticous, not awn-tipped.

Basal sheaths, blades, and culms moderately to densely villous.

Ligule about 1 mm. or less long; spikelets averaging 2 mm. long; awns of lemma 1 cm. or more long (Mexico: Chihuahua to Jalisco). **15. M. speciosa**

Ligule 1.5–6 (usually 2–4) mm. long; spikelets mostly 2–3 mm. long; awn of lemma lacking or, when present, up to 7 mm. long (Mexico: Chihuahua to Puebla) . . . . . **16. M. pubescens**

Basal sheaths, blades, and culms glabrous to scabrous, but never villous.

Lemma all or mostly glabrous (the hairs confined to the base of the margins or rarely present on the midnerve at the base), awnless or rarely short-awned; plants robust.

Sheath auricles present, about 3 mm. long; ligule mostly 2–3.5 mm. long; spikelets 2–3 mm. long, ashy gray or purple; lemma glabrous, the margins rarely pubescent at the base (Mexico [Nayarit south], Guatemala, and Nicaragua). . **17. M. robusta**

Sheath auricles lacking; ligule 4–12 (usually 4–8) mm. long; spikelets 3–3.6 mm. or more long, dark green; margins of lemma generally short-pilose at the base (Mexico: San Luis Potosíto Puebla) . . . . . **18. M. virletii**

Lemma pubescent on the midnerve or lower part to densely villous throughout, if glabrous, then long-awned.

Ligule a short rim, generally not over 5 mm. long.

Blade much narrower than the sheath at their juncture; old basal sheaths conspicuously brown, curled and fibrillose (Guatemala and Honduras). **19. M. breviligula**

Blade not much narrower than the sheath at their juncture, old basal sheaths not conspicuously brown, curled, and fibrillose.

Lemmas moderately pubescent or villous on and between the nerves (Mexico: Chihuahua to Puebla) . . . . . **16. M. pubescens**

Lemmas glabrous above, the pubescence confined to the very base of the margins and midnerve.

Culms glabrous below the nodes; ligule 0.3–1.5 mm. long; spikelets 2–2.2 mm. long; glumes slightly awn-tipped (Guatemala: Quezaltenango) . . . . . **20. M. aurea**

Culms pubescent below the nodes; ligule 1.5–6 mm. long; spikelets usually 1.5–2 mm. long; glumes acute or slightly erose (Mexico: Sinaloa to Jalisco) . . . . . **21. M. grandis**

Ligule often 1 cm. or more long, at least more than 5 mm. long.

Lemmas pubescent or villous on and between the nerves; spikelets usually 3 mm. or more long, green or greenish brown.

Lemmas densely villous throughout, with awns over 1 cm. long; panicles lead-green or purplish green (Mexico [Michoacán south] and Honduras). **9. M. versicolor**

Lemmas sparsely villous, awnless or short-awned (awns much less than 1 cm. long when present); panicles greenish brown or tan (Mexico [Durango south] and Guatemala). . . . . **22. M. distans**

Lemmas glabrous or pubescent on the midnerve and/or margins, but not (or hardly) pubescent between the nerves.

Spikelets 5–7 mm. long; glumes sparsely pubescent, awn-tipped (Mexico: Jalisco and Aguascalientes) . . . . . **23. M. longiglumis**

Spikelets 2–3 mm. long (rarely longer); glumes glabrous, muticous.

Palea pubescent between the keels; callus of floret truncate (southwestern United States to Oaxaca, Mexico) . . . . . **24. M. emersleyi**

Palea glabrous between the keels; callus of floret truncate or acute.

Glumes glabrous, shining, almost translucent, nerveless or indistinctly 1-nerved; panicle branches short, appressed; callus of floret truncate (Mexico: Chiapas) . . . . . **25. M. xanthodas**

Glumes scabrous, distinctly 1-nerved; panicle branches long, ascending or spreading; callus of floret acute (Costa Rica to Colombia). **26. M. lehmanniana**

1. Muhlenbergia gooddingii Soderstrom, sp. nov.

Perennis caespitosa, culmis erectis glabris, ca. 60–110 cm. altis, nodis 4, vaginis inferioribus teretibus compressis vel paullo carinatis glabris; ligula utrinque decurrente, basin versus firma fuscaque, alibi membranacea, margine versus apicem lacerata, ca. 15 mm. longa, laminis arcuatis ad apicem attenuatis, involutis, 50 cm. longis vel

longioribus, ca. 2 mm. latis, panicula densa nutante straminea vel purpureo-viridi, axe scaberulo, ramis primariis 3–9.5 (plerumque 3–5) cm. longis, secundariis plerumque 1–2 cm. longis, tertiariis ad 1 cm. longis, pedicellis scaberulis, 1–1.5 mm. longis, spiculis acutis 2–3 mm. longis, glumis acutis, nonnullis minute aristatis, plerumque aequalibus, quam flosculo longioribus, glabris vel scaberulis, nervis 0 vel 1 indistinctis, lemmatibus acutis glabris basin versus margine (et plerumque in nervo centrali) puberulis, palea glabra.

A *M. emersleyi* Vasey vaginis magis teretibus, ligula utrinque decurrente, laminis involutis arcuatisque, lemmatibus minus pubescentibus, et palea glabra differt.

Caespitose perennial; culms 60–110 cm. tall; nodes 4, glabrous below; basal sheaths rounded to strongly compressed, rarely slightly keeled, glabrous, stramineous, inflated when old; ligule firm, brown, and broadly decurrent at the base, becoming more membranous and lacerate above, the firm lower part 4–7 mm. long, the upper membranous part 1 cm. or longer; sheath auricles lacking; blades of the culm long and narrow, becoming filiform, conduplicate or somewhat involute when dry, 50 cm. or longer, about 2 mm. wide when unfolded, upper surface of blade scaberulous or scabrous, the lower surface scabrous, the blades when old firm, brown, and strongly arcuate at the base; upper throat glabrous to scaberulous; collar glabrous.

Panicle narrow, nodding, the branches appressed or ascending, dense, stramineous or light purplish green, 22–45 cm. long, 2–4 cm. wide; axis scaberulous; primary branches mostly 3–5 (rarely as much as 9.5) cm. long, floriferous to near the base, the secondary branches mostly 1–2 cm. long, tertiary branches lacking or, when present, 1 cm. or less long; pedicels 1–1.5 mm. long, scaberulous; spikelets 2–3 mm. long (averaging 2 mm. in the holotype); glumes equal or the second a little longer than the first, acute, dentate, many bearing a tiny awn, glabrous or punctate-scaberulous, nerveless or indistinctly 1-nerved; lemma a little shorter than the glumes, acute, mostly glabrous except for sparse hairs toward the base of the lateral margins and/or midnerve, 3-nerved, excurrent from below the tip as a flexuous yellow or purple awn 1 cm. or longer; palea about equal to the lemma, glabrous or rarely with sparse short hairs between the keels toward the base.

Holotype in the herbarium of Yale University; collected in canyon north of Moristo Canyon, Baboquivari Mountains, altitude 4,000 ft., November 19, 1945, by Leslie N. Goodding (No. 462–45). Isotypes at ARIZ and NY.

DISTRIBUTION: Restricted in range—collected in mountains near the Mexican border in the southernmost Arizona counties of Cochise, Pima, and Santa Cruz, at elevations of 3,000–7,000 ft. Of the two

additional collections from Sonora, Mexico, one is questionably *M. gooddingii.*

UNITED STATES: ARIZONA: COCHISE COUNTY: West slope of Mule Mountains, *Goodding* M–345 (ARIZ), M–346 (ARIZ); Garden Canyon, Huachuca Game Reserve, *Goodding* 586–49 (ARIZ); Dragoon Mountains, *Goodding* 50–56 (ARIZ); Mule Mountains, *Goodding* 307–61 (ARIZ), 451–61 (ARIZ); Fort Huachuca Military Reservation, *Goodding* 271–62 (ARIZ). PIMA COUNTY: Quinlin Mountains, *Goodding* 179–45 (ARIZ); Baboquivari Peak, *Goodding* 281–45 (ARIZ, NY, YU); Moristo Canyon, Baboquivari Mountains, *Goodding* 408–45 (ARIZ, NY, YU), 457–45 (ARIZ, NY, YU), 460–45 (ARIZ, YU), 468–45 (ARIZ, NY, YU); Canyon N. of Moristo Canyon, Baboquivari Mountains, *Goodding* 462–45 (YU holotype, ARIZ, NY, isotypes); Coyote Mountains, *Goodding & Hevly* 53–57; (ARIZ); Quinlin Mountains, *Goodding & Lusher* 179–45 (NY, YU). SANTA CRUZ COUNTY: Sycamore Canyon, *Goodding* CG–18 (US, YU), 2996 (UNM), M–394 (ARIZ, YU), G14–40 (YU).

MEXICO: SONORA: El Cañon de la Bellota, Sierra de la Cabellera, *Santos* 2110 (SMU, TEX, US);(?) N. of Babiacora on road to Cumpas, *Wiggins* 7393 (ARIZ, DS, MICH, UC, US).

This species superficially resembles some forms of *M. emersleyi,* as most of the collections have been named. It differs in the rounded or compressed, but rarely keeled, basal sheaths, firm ligules brown below and membranous above, and long-attenuate blades becoming threadlike or filiform. The old blades are usually arcuate at the base. Of the spikelet features to distinguish the species, the lemma and palea are significant; in *M. gooddingii* the hairs on the midnerve and margins are sparse and confined to the lower part and the palea is glabrous between the keels. The panicles of *M. gooddingii* are narrow and densely flowered and the lemmas are always awned. Such plumelike panicles among the filiform foliage probably create a distinctive look to this species in the field.

Muhlenbergia gooddingii cannot be called a typical member of section *Epicampes* because its features of the firm ligule, brown below, and the more or less rounded basal sheaths are characteristic of the *Podosemum* section.

Because of its combination of characters a possible ancestry is suspected in *M. emersleyi* and *M. longiligula,* for the new species occurs in the overlap of range of the other two species and *M. gooddingii* has features of both. A comparison of many characters from descriptions in this paper illustrates the intermediate position of *M. gooddingii,* as shown below:

	M. emersleyi	*M. longiligula*	*M. gooddingii*
culms	1–1.5 (occasionally to 2) meters	60–130 (100) cm.	60–110 cm.
nodes	3–4, glabrous or somewhat puberulent below	1 or 2 on lower part, glabrous	4, glabrous below

	M. emersleyi	*M. longiligula*	*M. gooddingii*
basal sheaths	compressed, keeled, glabrous	rounded, rarely compressed, but never keeled; scaberulous; old sheaths expanded	rounded to strongly compressed, rarely slightly keeled; glabrous; old sheaths expanded
ligule	membranous, usually a little firmer at base than above where thin and usually lacerated into narrow strands	firm, brown, decurrent, sometimes becoming membranous at tip	firm, brown, broadly decurrent at base, becoming membranous and lacerate above
blades	2–6 mm. wide, flat or folded, 23–47 (mostly 20–40) cm. long	long-attenuate to a brown, pointed tip, flat or inrolled at edges; to 65 (20–40) cm. long, 3–5.5 (usually about 4 mm.) wide	long, narrow, becoming filiform; conduplicate or somewhat involute when dry; 50 cm. long, about 2 mm. wide
blade surface	upper: glabrous to scaberulous	upper: glabrous to scaberulous (mostly scaberulous)	upper: scaberulous or scabrous
	lower: scabrous	lower: mostly scabrous	lower: scabrous
old blades	brown, not especially firm, not arcuate	brown, firm, folded and somewhat arcuate	firm, brown, strongly arcuate at base
panicle	typically lax above, branches loosely ascending or spreading; light purple to purplish tan	erect, narrow greenish to purple	nodding, the branches appressed or ascending, dense, stramineous or light purplish green
panicle dimensions	20–40 (mostly 30–40) cm. long, 4–7 cm. wide (more in field)	15–55 (30–45) cm. long, 1–5 (generally 1.5–2) cm. wide	22–45 cm. long, 2–4 cm. wide
1° branches	9–17 (9–12) cm. long	to 13 (generally 3–5) cm. long	3–5 (to 9.5) cm. long
2° branches	3–9 (3–5) cm. long	to 5 (generally 1–2) cm. long	1–2 cm. long
3° branches	0.5–4.5 (0.5–1.5) cm. long	lacking	lacking or to 1 cm. long
spikelets	2.2–3.2 (2.5–2.7) mm. long	2–3.5 (usually 2.5–3) mm. long	2–3 (2) mm. long

	M. emersleyi	*M. longiligula*	*M. gooddingii*
glumes	broadly acute	acutish, sometimes midnerve extending into a minute awn	acute, dentate, many bearing a tiny awn
lemma	acutish; pubescent on midnerve and margins ½–¾ their length	glabrous (rarely scaberulous)	mostly glabrous except for sparse hairs toward base of margins and/or midnerve
awn of lemma	0 to 1.5 cm. long	rarely a minute awn present	1 cm. or more long
palea	pubescent between the keels ½–¾ their length	glabrous	glabrous or rarely with sparse short hairs between the keels toward the base

This species, with a few exceptions, has been collected by Mr. Leslie N. Goodding, a long-time resident of Arizona, staunch conservationist, and botanist keenly interested in the Arizona flora. It is a pleasure to recognize Mr. Goodding's interest in grasses and contributions to Arizona botany by naming for him this predominantly Arizona species.

2. Muhlenbergia longiligula Hitchc. Amer. Journ. Bot. 21:136. 1934.

Epicampes ligulata Scribn. *in* Vasey, Contr. U.S. Nat. Herb. 3(1):58. 1892. Basis of *Muhlenbergia longiligula* Hitchc., not *M. ligulata* Scribn. and Merr. (*Pringle*, Santa Rita Mts., Arizona, July 26, 1884, selected by A. S. Hitchcock as lectotype).

Epicampes anomala Scribn. *in* Beal, Grasses N. Amer. 2:311. 1896. (*Pringle* 1423, Arroyo Ancho, Sierra Madre, Chihuahua, Mexico). Not *Muhlenbergia anomalis* Fourn. 1896.

Epicampes distichophylla var. *mutica* Scribn. *in* Beal, Grasses N. Amer. 2:308. 1896 (*Toumey* 740, July 23, 1892, Arizona).

Epicampes stricta var. *mutica* Jones. Contr. West. Bot. 14:6. 1912. Based on *E. distichophylla* var. *mutica* Scribn.

Strongly caespitose perennial; culms glabrous, becoming scaberulous toward the panicle, 60–130 cm. (usually about 1 meter) tall; nodes 1 or 2, on the lower part, glabrous; basal sheaths rounded, rarely compressed, but never keeled, glabrous to scaberulous, loosely imbricate, the old sheaths expanded, yellowish brown, persistent; ligule firm, brown, decurrent, sometimes becoming membranous at the tip, especially in the uppermost blades of the culm, 1–3 (usually 1–1.5) cm. long, distinctly 2-keeled when large and broad; sheath auricles lacking; blades of the culm to 65 (usually 20–40) cm. long, long-attenuate to a brown, pointed tip, flat or inrolled at the edges, 3–5.5 (usually about 4) mm. wide when flat, the uppermost blade of the culm beneath the panicle short, the upper surface of the blade glabrous to scabrous

(mostly scaberulous), the lower surface mostly scabrous, the old blades brown, firm, folded, and somewhat arcuate at the point of attachment to the sheath; upper throat glabrous; collar glabrous (rarely scaberulous).

Panicle erect, narrow, the panicle branches borne in bunches along the axis, branches of the lowest cluster shorter than the clusters above, an interruption usually present between the basal and remaining clusters, greenish to purple, 15–55 (usually 30–45) cm. long, 1–5 (usually 1.5–2) cm. wide; axis glabrous to scabrous (mostly scabrous), the primary branches to 13 (usually 3–5) cm. long, the secondary branches to 5 (usually 1–2) cm. long, bearing spikelets almost to the point of attachment of the secondary with the primary branches, tertiary branches lacking; pedicels very short, glabrous to scaberulous (rarely scabrous); spikelets 2–3.5 (mostly 2.5–3) mm. long; glumes usually longer than the floret, but often shorter, especially in the longer spikelets, usually equal or the second a little longer than the first, glabrous to scaberulous, acutish at the tip, sometimes extending into a minute awn, nerveless or 1-nerved; lemmas 2.5–2.9 mm. long, glabrous (rarely scaberulous), indistinctly 3-nerved, rarely with a minute awn; palea equal to or often a bit longer than the lemma, glabrous.

Lectotype in the U.S. National Herbarium, no. 746686, collected in the Santa Rita Mountains, Arizona, elev. 4,000 ft., July 26, 1884, by C. G. Pringle (without number). Hitchcock has written on the type sheet, "Selected as probable type. The Texas specimens are different and do not agree with the description. Note long firm ligule." Isolectotypes at F, GH.

DISTRIBUTION: Rocky mountain slopes and canyons, at elevations of 5,000–9,000 feet, most frequently found in exposed areas of the pine-oak zone at 6,000–8,000 feet, occasionally in lightly frosted areas where more shaded. Rather common from New Mexico to Arizona into northern Mexico, occurring in Sonora, Chihuahua, and Durango. Also reported from western Texas and southern Nevada.

UNITED STATES: NEW MEXICO: Mountains W. of Gray, *Goodding* M–252 (ARIZ, US), M–254 (ARIZ). CATRON COUNTY: Apache National Forest, *Laney* 16 (UNM); *Solheim & Solheim* 2343 (GH). Mangas, *Metcalfe*, Sept. 14, 1897 (GH, NY, US). GRANT COUNTY: Black Range, *Goodding & Goodding* 367 (ARIZ). Santa Rita del Calve, *Wright* 1973 (CAS, GH, MO, NY, UC, US). GREENLEE COUNTY: Castle Creek, Apache, *Utzat* 14 (UNM). SOCORRO COUNTY: Mogollon Mountains, *Metcalfe* 556 (ARIZ, GH, MO, NY, POM, US). ARIZONA: *Emersley* 47 (US). Upper Oak Creek, *Fulton* 7345 (ARIZ). Peña Blanca Mountains, *Goodding*, Sept. 20, 1935 (ARIZ); *Jones*, Sept. 20, 1884 (US). Rocky Canyon, *Rothrock*, in 1874 (F, GH, NY). Oak Creek Canyon, *Weatherwax* 2782 (TAES). APACHE COUNTY: Diamond Creek, *Gould & Robinson* 5030 ARIZ, NY, TAES). Reservation Ranch, *Wasser*, Aug. 1936 (ARIZ). COCHISE COUNTY: Chiricahua Mountains, *Blumer* 189 (ARIZ). Barfoot Park, *Blumer*

1424 (ARIZ, DS, F, GH, MO, NY, US). Herb Martyr Dam Area, "*Chiricahua Vegetation Team*" 59–803 (ARIZ). Carr Canyon, *Darrow, Gould, Phillips, & Pultz* 1437 (MO). Rock Canyon, Huachuca Game Reserve, *Goodding* 884–49 (ARIZ). Fort Huachuca Military Reservation, *Goodding* 568–58 (ARIZ, YU), 720–58 (YU). Pinery Pass, *Goodding & Goodding* 463 (ARIZ, UC). Carr Canyon, *Gould, Darrow, Pultz & Phillips* 2461 (CAS, UC, US). Divide between Carr and Ramsey Canyons, *Gould & Haskell* 3363 (ARIZ, NY, UC, US). Rucker Canyon, *Gould & Haskell* 4585 (ARIZ, GH). Bowie, *Jones* 4290 (ARIZ, POM, SMU, US). Huachuca Mountains, *Jones*, Sept. 3, 1903 (POM); *Lemmon & Lemmon* 2921 (GH), Sept. 1882 (US). Pine Canyon, *Toumey*, Sept. 10, 1896 (US). COCONINO COUNTY: Long Valley Ranger Station, Coconino National Forest, *Darrow* 3262 (ARIZ, CAS, US). Pine Flat Camp, Oak Creek Canyon, *Darrow*, Sept. 16, 1943 (ARIZ). GILA COUNTY: Mt. Ord, *Goodding* 123–47 (ARIZ). Young, *Goodding & Goodding* 341 (ARIZ). Long Valley, Pine-Winslow Road, *Goodding & Goodding* 354 (ARIZ). 5 mi. N. of McFadden Peak on Young Road, *Gould* 3915 (ARIZ, US). Workman Creek Canyon, *Gould & Hudson* 3793 (ARIZ, MO, UC, US). Cassadore Range, *Gould & Robinson* 4896 (ARIZ, UC). White Mountains, *Griffiths* 5367 (US), 5409 (GH, US), 5434 (US). GRAHAM COUNTY: 3 mi. SW. of Point of Pines, 70 miles E. of San Carlos, *Bohrer* 421 (ARIZ, CAS). Bluejay Ridge, *Gandy* 8 (UNM). Mt. Graham, *Hope* 9999 (ARIZ, MICH, US). GREENLEE COUNTY: Red Bluffs road above Blue, *Goodding & Goodding* 349 (ARIZ, US). Big Lue Range, *Gould & Haskell* 4064 (ARIZ, UC). 15 mi. N. of Blue, *Gould & Robinson* 5143 (ARIZ, TAES, UC). MARICOPA COUNTY: Sugar Loaf Mt. Wonderland of Rocks, *Darrow*, July 8, 1937 (ARIZ). NAVAJO COUNTY: Fort Apache, *Mayerhoff* 89 (F); *Schroeder*, in 1937 (ARIZ). PIMA COUNTY: Mt. Lemmon Road, *Benson* 9106 (ARIZ, DS, POM). Manning Camp, *Blumer* 3412 (ARIZ, DS, GH, MO, UC). Santa Catalina Mountains, *Brown* 135 (ARIZ), *Darrow*, Oct. 3, 1937 (GH). Prison Road, *Ginter*, Oct. 6, 1941 (UC). Moristo Canyon, *Goodding* 451–45 (ARIZ, NY). Santa Rita Mountains, *Griffiths & Thornber* 122 (US). Mt. Lemmon, Bear Canyon, *Hevly* 1028 (ARIZ). Santa Rita Mountains, *Kearney & Peebles* 10543 (ARIZ, MICH, US). Bigelow Tower, *Leader & Leader* 276 (ARIZ). San Luis Mountains, *Mearns* 373 (US). Rincon Mountains, *Nealley* 65 (NY, US), Aug. 1881 (GH, MO). Upper Bear Canyon, Santa Catalina Mountains, *Parker* 7099 (ARIZ). Mt. Lemmon, *Peebles & Harrison* 2294 (US); *Peebles, Harrison & Kearney* 2539 (ARIZ, US). Santa Rita Mountains, *Pringle*, July 26, 1884 (US lectotype, F, GH, isolectotypes). Madera Canyon, *Silveus* 3468 (TAES, TEX, US). Marshall Gulch, *Thornber* 2767 (ARIZ). Box Springs, *Thornber*, Aug. 10, 1906 (ARIZ). Tucson, *Toumey* 740 (DS, NY, US, isotypes of *E. distichophylla* var. *mutica*). SANTA CRUZ COUNTY: White House (Madera) Canyon, *Benson* 9780 (POM); *Gould* 2597 (ARIZ, UC, US); *Leader & Leader* 198 (ARIZ). Sycamore Canyon, *Goodding* M–111 (ARIZ), M–259 (ARIZ, US). Santa Rita Mountains, *Griffiths* 6074 (MO, US). Santa Catalina Mountains, *Thornber* 7689 (ARIZ). YAVAPAI COUNTY: Jerome, *Benham* M–34 ARIZ), M–105 (ARIZ); *Goodding* 75–46 (ARIZ). Mingus Mountain, *Benham* 43–B (ARIZ, MICH). Prescott, *Purchase* 513 (ARIZ).

MEXICO: SONORA: San José Mountains, *Marshall* 173 (ARIZ); *Mearns* 996 (US), 1649 (US). El Tigre, Rió de Bavispe, *Santos* 1963 (ARIZ, GH, MO, NY, SMU, TEX, US). El Picacho del Pilar, Río de Bavispe, *Santos* 2164 (GH, SMU) CHIHUAHUA: Between Río Chico and Río Caballo, *Barlow*, Sept. 30, 1911 (F, UC, US). Sánchez, *Hitchcock* 7667 (NY, US). Marsh Lake, *Jones*, Sept. 19, 1903 (POM). N. de Cd. Madera, *Martínez* F–2477 (CHAP, US). 35 km. SW. of Miñaca, *Pennell* 18928 (MEXU). NE. of Colonia Pacheco,

Pennell 19194 (US). Arroyo Ancho, *Pringle* 1423 (GH, US, isotypes of *E. anomala*) Sierra Madre, *Pringle* 1427 (F, GH, NY, US), 1703 (UC). 27 mi. NW. of Cd. Madera, *Reeder & Reeder* 2663 (YU). Ca. 43 mi. SW. of Casas Grandes, *Reeder & Reeder* 2692 (YU). 38 mi. S. of Casas Grandes, *Reeder & Reeder* 2699 (YU). 31 mi. W. of Colonia Juárez, *Reeder & Reeder* 3222 (YU). Palimos Cañon ca. 13 mi. E. of Chuhuichupa, *Reeder, Reeder, & Goodding* 1222 (YU). S. of Hernández, *Reeder, Reeder, & Soderstrom* 3505 (US, YU), 3509 (US, YU), 3531 (US, YU). DURANGO: 6.5 mi. W. of El Salto, *Reeder & Reeder* 2639 (YU). 25 mi. W. of Durango, *Reeder, Reeder, & Soderstrom* 3439 (US, YU).

Muhlenbergia longiligula is distinguished by its long, firm, decurrent ligule and rounded basal sheaths. On the basis of leaf anatomy, the long glumes, the dorsal awn (when present), and the general habit in the field, it seems to belong with the *Epicampes* section of *Muhlenbergia*. The firm ligule and rounded basal sheaths are also characteristics of species in the *Podosemum* section. Thus, *M. longiligula* possesses characters of both sections, and it appears to be more of a link between them than a distinct member of either. The closely allied species of the subgenus *Podosemum*, *M. lindheimeri*, *M. involuta*, *M. pubigluma*, and *M. reederorum*, all possess the decurrent ligule. Of these *M. involuta* and *M. reederorum*, like *M. longiligula*, lack strongly compressed-keeled sheaths. All occur within the same general range, *M. longiligula* ranging from southwestern United States into northern Mexico, *M. lindheimeri* in south-central Texas and Coahuila, *M. involuta* in Texas, *M. pubigluma* in Coahuila and Nuevo León, and *M. reederorum* in Durango, Mexico.

3. Muhlenbergia reederorum Soderstrom, sp. nov.

Perennis caespitosa, culmis angustis scabris, ca. 1 m. altis, basin versus nodis 3, puberulentis, vaginis inferioribus compressis et paullo carinatis glabris; collis scaberulis; ligula utrinque decurrente, basin versus firma et fusca, alibi membranacea et margine versus apicem lacerata, ca. 10–15 mm. longa; laminis culmi usque ad 65 cm. longis laete viridibus involutis, attenuatis et ad apicem filiformibus, laminis vetustis fuscis firmis arcuatis, ca. 1.5 mm. latis, utrinque scabris; panicula erecta, cetera laxa, laete viridi 30–47 cm. longa, quando appressa 2–3 cm. lata, axe scabro, ramis primariis 4–6 cm. longis, secundariis ca. 2 cm. longis, tertiariis ca. 5 mm. longis, pedicellis scaberulis, lateralibus 1.5–2.5 mm. longis, terminalibus 2–3 mm. usque ad. 6 mm. longis; spiculis lanceolatis 3.5–4.6 (plerumque 4) mm. longis, glumis acutis fere aequalibus, quam flosculo longioribus, scaberulis, nervis 0 vel 1, indistinctis, lemmatibus scaberulis, infra apicem minute aristatis, quam glumis paullo brevioribus.

A *M. involuta* Swallen vaginis magis carinatis, glumis quam lemmatibus paullo longioribus, spiculis longioribus, paniculis longioribus, et aristis quam lemmatibus brevioribus differt.

Caespitose perennial; culms rather slender, scabrous, erect, about 1 m. tall; nodes 3, puberulent below; basal sheaths compressed and somewhat keeled or compressed only, glabrous, purplish toward the base when young; collar scaberulous; ligule decurrent, the lower ½–¾ firm and brown, the upper half membranous and lacerate, about 10–15 mm. long; sheath auricles lacking; blades of the culm up to 65 cm. long, light green, tightly folded, long-attenuate becoming filiform, the old blades brown, firm and arcuate, about 1.5 mm. wide when flat, the upper and lower surfaces scabrous; upper throat scabrous.

Panicle erect, grayish green, 30–47 cm. long, 2–3 cm. wide when appressed, more open at anthesis; axis scabrous; branches of the panicle narrow, the primary branches 4–6 cm. long, secondary branches 1–2 cm. long, tertiary branches lacking or about 5 mm. long; pedicels evenly scaberulous, those of the lateral spikelets 1.5–2.5 mm. long, of the terminal spikelets 2–3 (to 6) mm. long; spikelets lanceolate, 3.5–4.6 (averaging 4) mm. long; glumes acute, about equal, scaberulous, nerveless or indistinctly 1-nerved; lemmas a little shorter than the glumes, scaberulous, 3-nerved, bearing a rudimentary awn 0.2–2.5 mm. long from just below the tip; palea glabrous.

Holotype in the Yale University Herbarium, collected in the Sierra Madre Occidental (W. of Ciudad Durango), 7 miles E. of Navíos, Durango, Mexico, elevation 7,700 ft., Sept. 26, 1963, by *J. R. & C. G. Reeder* (no. 3834). Isotypes at F, K, MEXU, MICH, NY, P, UC, and US.

Distribution: Known from Durango and possibly Jalisco, Mexico. The type specimen was collected in the Sierra Madre Occidental west of the city of Durango, where the large caespitose clumps are found on rocky canyon walls in the pine-oak zone at elevations of 7,700–8,800 ft.

MEXICO: Durango: 4 mi. W. of Navíos, *Reeder & Reeder* 4230 (US, YU); 7 mi. E. of Navíos, *Reeder, Reeder, & Soderstrom* 3436 (US, YU). 2 mi. SW. of Buenos Aires, *Reeder, Reeder, & Soderstrom* 3347 (YU). (?) Jalisco: Mountains N. of Autlán, 3–5 mi. above Mina San Francisco, *McVaugh* 19669 (MICH, US).

Muhlenbergia reederorum exhibits greatest similarity to *M. involuta*, known only in Texas. In *M. involuta* the basal sheaths are compressed, but not keeled; in *M. reederorum* they are usually more keeled, but the keel is not strong. In *M. reederorum* the glumes are a little longer than the floret, but much shorter in *M. involuta*, the spikelets are longer, averaging 4 mm., the panicle is longer, up to 47 cm., and the glumes are acute and entire at the apex. *Muhlenbergia longiligula* is also similar in many respects but its unawned lemmas and flat, wider (3–5.5 mm.) blades separate it from the new species. The many long, narrow blades of *M. reederorum* produce softer and more delicate

clumps in the field than the typical coarser clumps of other species of the *Epicampes* section. A unicate specimen (*Reeder, Reeder, & Soderstrom* 3347) collected near Buenos Aires, Durango, differs from the material of the type locality in the more membranous ligule, the longer awn of the lemma (up to 2 mm.), and the wider blades (up to 2.5 mm. wide).

This previously undescribed species is named in honor of Professor John R. Reeder of Yale University and his wife, Charlotte Goodding Reeder. Because of their interest in the Gramineae, especially of Mexico, and the genus *Muhlenbergia* it is appropriate that a *Muhlenbergia* from that country bear their name.

4. Muhlenbergia involuta Swallen. Amer. Journ. Bot. 19: 436. *f. 2.* 1932.

Caespitose perennial; culms glabrous or scaberulous at the base, to 135 (usually 70–100) cm. tall; nodes 4 or more, mostly glabrous or puberulent beneath; basal sheaths compressed, but not strongly keeled, tightly imbricate, yellowish brown, not becoming fibrillose when old; ligule decurrent, firm and brown at the base, becoming acute and membranous only toward the tip, often firm about three-quarters of its length, membranous one-quarter of the length, to 1.2 cm. long; sheath auricles lacking; blades of the culm to 45 cm. long, pale green, often arcuate, long-attenuate to a firm point, tightly folded, 1–2 mm. wide when unfolded, the upper surface of the blade scabrous, bearing a mat of numerous tightly appressed white hairs (spicules), the lower surface of the blade scabrous; upper throat scabrous; collar scaberulous.

Panicle erect, greenish to tan, to 40 (usually 20–30) cm. long, 1.5–7 cm. wide, branches of the panicle long; axis scabrous, the primary branches 6–9 (usually 6–8) cm. long, the secondary branches 1–4 (usually 2–3.5) cm. long, the tertiary branches to about 2 (usually 1 or less) cm. long; pedicels of the terminal spikelets very long, equaling the spikelet or, more often, much longer, pedicels of the lateral spikelets usually shorter than the spikelet; spikelets 3–4 (averaging 3.5) mm. long; glumes equal or the second 1 mm. or more longer than the first, slightly toothed at apex, occasionally bearing a rudimentary awn, usually glabrous but sometimes scaberulous, 1-nerved; lemmas 3.2–4.2 (usually 3.5) mm. long, usually much longer than the glumes, rarely about equal, glabrous or with a few hairs at the base of the lateral margins, rather strongly 3-nerved, awned, the awns 1–2.4 (usually 1–2) mm. long; palea about equal to lemma, glabrous.

Type in the U.S. National Herbarium, no. 1501594, collected on draws in hills, 20 miles NE. of San Antonio, Texas, Oct. 10–31 (year not cited), by W. A. Silveus (no. 358).

DISTRIBUTION: Rocky banks and draws of hills, usually on limestone soil. Of very limited distribution, in south-central Texas.

UNITED STATES: TEXAS: BANDERA COUNTY: Bandera, *Silveus* 7393 (TEX). BEXAR COUNTY: Hills NE. of San Antonio, *Silveus* 314 (TEX, US). 20 mi. NE. of San Antonio, *Silveus* 358, = *Amer. Gr. Nat. Herb.* 1324 (US Holotype, CAS, GH, LL, MO, SMU, UC, isotypes). BOERNE COUNTY: Open calcareous hillsides, *Palmer* 10829, in 1916 (US). BURNET COUNTY: S. of Burnet, *Silveus* 7676 (ARIZ, CAS, DS, SMU, TAES, TEX). HAYS COUNTY: W. of Cedar Valley, Edwards Plateau, *Gould* 5336 (TAES). KENDALL COUNTY: Spanish Pass, *Cory* 26212 (TAES, US). SW. of Boerne on the Boerne-Bandera road, *Silveus* 780 (TEX, US). Comfort, *Silveus* 2335 (CAS, TAES, TEX), 7339 (CAS, TAES, TEX). KERR COUNTY: NW. of Kerrville, *Reed*, Sept. 28, 1937 (US). TRAVIS COUNTY: W. of Trading Post on cut off road to Pedernales Bridge, *Brown* 50–323 (SMU, TAES, TEX). Glen Rose, W. of Austin, *Moon* 167 (TEX). Austin, *Tharp* 3968 (TEX), 5198 (TEX). Pedernales road, 8 mi. W. of Bee Cave, *Tharp* 53–250 (TEX). W. of Austin, *Warnock* 45–27 (TEX, US). Hamilton Pool, *Webster* 1961 (TEX).

Muhlenbergia involuta is distinguished by its firm, decurrent ligule, in combination with the compressed but not keeled basal sheaths, the tightly folded arcuate blades, and glabrous lemmas that usually exceed the glumes in length. Swallen, in describing this species, remarked, "*Muhlenbergia involuta* is related to *M. distichophylla* (Presl) Kunth but in that species the spikelets are only 1.5–2 mm. long, the awns are 10–15 mm. long, the blades are flat, as much as 5 mm. wide, and the sheaths bear auricles 2–3 cm. long. In both species the glumes are shorter than the floret." However, *M. involuta*, is by no means closely related to *M. distichophylla*. The latter is allied to *M. macrotis* and *M. robusta* in which the sheaths bear rudimentary to very long auricles, the lemmas are glabrous, and the ligule membranaceous throughout. In *M. involuta* the ligule is decurrent, very firm and brown at the base, becoming membranaceous only at the tip. This character, in addition to the pale green, firm, tightly folded arcuate blades, indicates that it is closer to *M. lindheimeri*, *M. pubigluma*, and *M. reederorum*. *Muhlenbergia involuta* is endemic to Texas, *M. lindheimeri* to Texas and Coahuila, *M. pubigluma* is known only from Coahuila and Nuevo León in northern Mexico, and *M. reederorum* only from Durango (and possibly Jalisco), Mexico. The distribution of these species in Texas, Coahuila, and Durango separates them from *M. distichophylla* from farther south, Jalisco, Mexico, into Guatemala.

5. Muhlenbergia lindheimeri Hitchc. Journ. Washington Acad. Sci. 24(7):291. 1934.

Epicampes gracilis Trin. Mem. Acad. St. Petersb. VI. Sci. Nat. 4:271. 1841. Fragments of panicle of this specimen ex Trinius herbarium (LE), in type collection at the U.S. National Herbarium marked "*Epicampes gracilis* in 'Mexico de Karwinsky.' Hb. Reg. Monac (Munich) no. 595." The published locality of this specimen is Mexico, but the species is known only

from south-central Texas. This reference is doubtless made to territory now Texas but which was still part of Mexico in 1841. Not *Muhlenbergia gracilis* (H. B. K.) Kunth. 1829.

Strongly caespitose perennial; culms stout, robust, glabrous, 0.5–1.5 (mostly more than 1) meters tall; nodes 4, glabrous beneath the nodes; basal sheaths compressed-keeled, glabrous, tightly imbricate and usually yellowish or purplish brown; ligule decurrent, firm and brown at the base, becoming membranous above, usually enclosed within the tightly folded blade, up to 3.5 (mostly 1–1.5) cm. long; sheath auricles lacking; blades of the culm 25–55 (usually 30–45) cm. long, narrow, pale green, very firm and conduplicate, 2–4 (usually 2–3) mm. wide when flat, the upper surface of the blade scabrous, bearing a tight mat of dense short white hairs, the lower surface scaberulous to scabrous; upper throat scabrous, bearing a dense mat of short white hairs; collar glabrous to scaberulous.

Panicle erect, narrow, pale green or tan, the panicle branches floriferous almost to the base, occurring in bunches at intervals along the axis, the naked portion of the axis sometimes obvious, sometimes obscured by the overlapping appressed panicle branches, to 50 (mostly 20–30) cm. long, 1–3 (mostly 1.5–2) cm. wide; axis scabrous, the primary branches to 5 (mostly 2–4) cm. long, the secondary branches to 1.5 (mostly 0.5–1.5) cm. long, tertiary branches lacking; pedicels of the lateral spikelets to 0.5–1.2 (usually 0.5–0.8) mm. long, those of the terminal spikelets to 3 mm. long, scabrous; spikelets 2–3.5 (usually 2.5–3) mm. long; glumes about equal to (sometimes shorter than) the floret, the second a little longer than the first, glabrous to scabrous (mostly scabrous), rounded at the tip or blunt, rarely acute except in the longer spikelets, awnless, strongly 1-nerved; lemmas to 3 (mostly 2.4–2.6) mm. long, glabrous or rarely puberulent at the base, mostly rounded at the tip, 3-nerved (the nerves purple), awnless or rarely with awns as much as 4 mm. in length; palea a little shorter than the lemma, glabrous or occasionally with a few minute hairs at the base between the purplish keels.

Holotype in the U.S. National Herbarium, no. 998949, collected in 1847 by Ferdinand Lindheimer in Texas. Only the number 725 is given, this being the number of the "Plantae Lindheimerianae" series. According to Blankinship (1907) this represents Lindheimer's own collecting number of 465 (fasc. IV) and was collected in Friederichsburg (now Fredericksburg), Gillespie County, Texas, in September 1847. Isotypes at F, GH, MO, and UC.

DISTRIBUTION: Dry sandy or limestone soil, in draws of hills and open areas. Of limited distribution in south-central Texas and Coahuila, Mexico.

UNITED STATES: TEXAS: Southern Texas, *Lindheimer*, in 1849–51 (NY); *Nealley*, in 1889 (GH). Foothills, upper Seco, *Reverchon* 1610 (F, MO, NY, TEX, US). Glen Rose Hills, *Tharp* 46293 (TAES, UC), *Tharp*, Dec. 7, 1928 (MO, NY, SMU). BANDERA COUNTY: N. of Medina, *Parks & Cory* 24422 (TAES). W.–NW. of Bandera, *Shinners* 16880 (SMU). BELL COUNTY: Maxdale, *Wolff* 2632 (TAES, US). BEXAR COUNTY: Onion Creek, near San Antonio, *Brown* 3487 (TEX). Pleasonton Road 15 mi. S. of San Antonio, *Burr* 513 (NY). Cibolo Creek, *Liles* 17 (TAES). North Loop, *Silveus* 11 (TEX, US), 355 (TEX, US). 20 mi. NE. of San Antonio, *Silveus* 354 (MICH, TEX, US). BURNET COUNTY: NE. of Lake Buchanan toward Lampasas, *Whitehurst*, Nov. 21, 1956 (LL). COMAL COUNTY: Comanche Spring, New Braunfels, etc., *Lindheimer* 1255 (ARIZ, F, GH, NY, TEX, UC, US). COMANCHE COUNTY: Comanche Spring, *Lindheimer* 176 (CAS, ILL, MO, TAES). EDWARDS COUNTY: Barksdale, *Palmer* 11004, in 1916 (MO, US); *Parks & Cory* 26893 (TAES). GILLESPIE COUNTY: Fredericksburg, *Thurber* 68 (NY). *Lindheimer* 465, = *Plantae Lindheimerianae* 725 (US holotype, F, GH, MO, UC, isotypes). HAYS COUNTY: Reagan Houston Ranch, *Johnson* 360 (TEX). KENDALL COUNTY: N. of Comfort, *Cory* 20732 (GH, UC); *Parks & Cory* 20729 (TAES), 20730 (TAES), 20731 (TAES). Spanish Pass, *Palmer* 10859, in 1916 (US). Comfort, *Silveus* 7334 (CAS, DS, SMU, TAES, TEX). KERR COUNTY: Kerrville State Park, *Cory* 50506 (DS, GH, NY, SMU, TAES, TEX, UC, US). 25 mi. NW. of Kerrville, *Gould* 8468 (SMU, TAES, UC). SW. of Kerrville, *Parks & Cory* 24840 (TAES). KIMBLE COUNTY: NE. of junction on Mason Highway, *Landers* 5223 (TAES). KINNEY COUNTY: W. of Bracketville, *Correll & Correll* 24740 (LL). MASON COUNTY: N. of Mason, *Reardon* 23 (TAES). REAL COUNTY: W. Fork of West Frio River, *Cory* 43240 (SMU, TEX). N. of Leakey, *Parks & Cory* 27385 (TAES). TRAVIS COUNTY: Austin, *Bodin*, Oct. 20, 1891 (DS). Oak Hill, *Rogers* 6520 (TEX). Barton Creek, Austin, *Tharp* 70 (TEX, US). Edwards Plateau, *Tharp* 3076 (US). Watkins Ranch, *Tharp* 49009 (US); *Tharp, Rogers, Wilkins, Cowan, Clark & Jeffrey* 49004 (TEX, US); *Tharp et al.* 51–516 (TEX). Austin, *Warnock* W1065 (TEX, US). WILLIAMSON COUNTY: Georgetown, *Bodin* 287 (NY).

MEXICO: COAHUILA: About 24.5 mi. SW. of Piedras Negras, *Reeder & Reeder* 3921 (US, YU). 8 mi. W. of Cuatro Cienegas, *Reeder & Reeder* 3945 (US, YU).

Muhlenbergia lindheimeri is distinguished by the decurrent ligule, long spikelets with glabrous lemmas, the glumes equal the floret, and the long-attenuate firm blades somewhat arcuate when old. It appears to be most closely related to *M. involuta* and *M. pubigluma*. The former differs in having basal sheaths somewhat compressed but not keeled and glumes shorter than the floret, the latter in having puberulent glumes and lightly villous lemmas.

6. Muhlenbergia pubigluma Swallen. Proc. Biol. Soc. Wash. 56:78. 1943.

Strongly caespitose perennial; culms stout, glabrous, about 75–125 cm. tall; nodes 3, pubescent below; basal sheaths compressed-keeled, glabrous, tightly imbricate, the old basal sheaths firm, dark brown, not becoming fibrillose; ligule decurrent, firm and brown at the base, becoming membranous for the greater part of its length, 5–13 mm. long, longer on the innovations; sheath auricles lacking;

blades of the culm to 35 cm. long, narrow, pale green, firm and conduplicate, long-attenuate to a firm brown point, 1–2 mm. wide when flat, the upper surface of the blade scabrous, bearing a tight dense mat of tiny white hairs, the lower surface scabrous; upper throat bearing a dense mat of short appressed hairs; collar scaberulous.

Panicle erect, narrow, the branches appressed, interrupted below, olive to grayish green, 20–34 cm. long, 1–2 cm. wide; axis scabrous; lower primary branches 4–5 cm. long, the secondary branches to 1.5 cm. long, tertiary branches lacking; pedicels much shorter than the spikelets, scabrous; spikelets 2.5–3.5 (averaging 3) mm. long; glumes rounded at the tips, mostly longer than the floret, the second a little longer than the first, hyaline, nerveless or indistinctly 1-nerved, lightly pubescent, awnless; lemmas 2.9–3.1 mm. long, acute at the tip, indistinctly 3-nerved, awns 0.5–3.5 mm. long, the lower two-thirds lightly villous, the upper one-third scabrous, the basal margins more densely villous; palea a little shorter than the lemma, pubescent on the lower two-thirds between the keels.

Holotype in the U.S. National Herbarium, no. 2209360, collected in shrub zones of lower canyon where common, Sierra de la Madera, Cañon del Agua, Municipio de Cuatro Cienegas, Sept. 10, 1939, by C. H. Muller (no. 3264).

DISTRIBUTION: Known only from five collections made in canyons of Coahuila and Nuevo León, northern Mexico.

MEXICO: COAHUILA: La Cueva, Corte Blanco fork of Charretera Canyon, *Johnston* 9072 (GH, MEXU, MO). Cañon del Agua, Municipio de Cuatro Cienegas, *Muller* 3264 (US holotype, GH, UC, isotypes). San Lorenzo Canyon, 6 mi. SE. of Saltillo, *Palmer* 401, in 1904 (F, GH, MO, NY, UC, US). NUEVO LEÓN: Between La Soledad and Escondida, *Beetle* M–406 (UC). 14 mi. W. of Doctor Arroyo, *Shreve & Tinkham* 9651 (GH).

Muhlenbergia pubigluma is distinguished by the broadly decurrent ligule, puberulent glumes and lightly villous lemmas. In the original description, the author related this species to *M. pubescens* (H.B.K.) Hitchc. (=*M. distans* Swallen, according to the present treatment). That species, however, does not have the narrow, firm, pale green, somewhat arcuate blades or broadly decurrent, firm at the base, ligules, characters that indicate a closer relationship to *M. lindheimeri* and *M. involuta*.

7. Muhlenbergia macrotis (Piper) Hitchc. N. Amer. Fl. 17(6):463. 1935.

Muehlenbergia distichophylla var. *mutica* Scribn. ex Urbina. Cat. Pl. Mex. 393. 1897. Nomen nudum. Of the two collections listed, *Pringle* 2360=*M. macrotis*, and *Pringle* 5577=*M. versicolor*.

Epicampes macrotis Piper. Proc. Biol. Soc. Washington 18:144. 1905. Basis of *Muhlenbergia macrotis* (Piper) Hitchc. (*Rose* 3528, Zacatecas, Mexico.)

Epicampes minutiflora Mez. Repert. Sp. Nov. Fedde 17:212. 1921. Basis of *Muhlenbergia meziana* Hitchc. 1935, not of *M. minutiflora* (Michx.) Hitchc. 1896. (*Langlassé* 750, El Canizal, "Michoacán et Guerrero," Mexico.)

Muhlenbergia meziana Hitchc. N. Amer. Fl. 17(6):461. 1935. Based on *Epicampes minutiflora* Mez.

Strongly caespitose perennial; culms narrow to very thick, glabrous to scaberulous, 1¼–2¼ meters tall; nodes 3–5, glabrous, or sometimes pubescent below the nodes; basal sheaths compressed-keeled, glabrous, the old basal sheaths brown, persistent, becoming frayed; ligule membranous throughout, lacerate from the base or near the base, 3–15 (usually 5–8) mm. long; sheath auricles 1–10 (usually about 3) cm. long, the auricles of the sheaths higher on the culm often longer than those of the lower ones, straight or strongly twisted; blades of the culm very long, as much as 95 cm., becoming fine and threadlike at the tip, mostly folded, 2–6 mm. wide when flat, the blades at the base narrower than the sheaths, edges of the blades saw-toothed, the upper surface scaberulous to scabrous (mostly scabrous), the lower surface scabrous; upper throat scabrous; collar glabrous.

Panicle erect, columnar, the branches numerous, appressed, generally interrupted below, light green to whitish green, 25–65 cm. long, 1.5–6 cm. wide; axis scaberulous to scabrous (mostly scabrous), the primary branches 5–12 cm. long, the secondary branches to 4.5 cm. long and spikelet-bearing to the base, the tertiary branches to 1 cm. in length; pedicels 0.3–1 mm. long, shorter than the spikelets, scabrous; spikelets 2–3 mm. long, rarely as short as 1.5 mm. or longer than 3 mm.; glumes equal, usually longer than the floret, glabrous to scaberulous (mostly scaberulous), rounded at the tips, awnless, hyaline, white or whitish green, nerveless or obscurely 1-nerved; lemmas 1.8–2.5 mm. long, acutish, indistinctly 3-nerved, awnless or rarely cuspidate, completely glabrous, even on the lower margins, at most the surface punctate; palea equaling the lemma or rarely a little longer, glabrous.

Holotype in the U.S. National Herbarium, no. 302505, collected in the Sierra Madre, Zacatecas, Mexico, Aug. 17, 1897, by J. N. Rose (no. 3528).

DISTRIBUTION: Moist shaded canyon slopes, ravines, banks above streambeds, moist ditches, and wooded hillsides, at elevations of 6,000–7,000 feet. Common from Sinaloa and Durango, south to Guerrero and Oaxaca, Mexico. A single specimen has been collected in Guatemala.

MEXICO: SINALOA: Mazatlán, *Ortega* 5075 (US). DURANGO: Sierra Tres Picos, *Gentry* 5312 (ARIZ, DS, MO, NY); *Harvey* 5312 (GH). 23 mi. SW. of

Buenos Aires, *Reeder & Reeder* 4218 (US, YU). ZACATECAS: Sierra Madre, *Rose* 3528 (US holotype). NAYARIT: La Barranca, *Jones* 23445 (CAS, MO, NY, POM). SINALOA-NAYARIT: San Ignacio, San Javier, *Ortega* 1204 (MEXU). JALISCO: Tepatitlán-Guadalajara, *Hernández, Ruppert, & Guevara* X–2669 (US). SW. Autlán, *Hernández* X. 4641 (CHAP). La Barranca, Guadalajara, *Jones* 27656 (POM), 27677 (DS, MO, NY). Orendain, *Jones* 2767 (UC). Nevado de Colima, *McVaugh* 10170 (MICH). Sierra del Tigre, 3 mi. S. of Mazamitla, *McVaugh* 13085 (SMU, US). 1–2 mi. E. of Tapalpa, *McVaugh* 20519 (MICH, US). Real Alto, Trail to Tranquillas, *Mexia* 1713 (CAS, DS, F, GH, MICH, MO, NY, UC, US). Guadalajara, *Pringle* 2360 (ARIZ, CAS, F, GH, MICH, NY, TAES, UC, US), 2356 (F, GH, MO, NY, UC, US); *Soderstrom* 613 (US), 614 (US). GUANAJUATO: *Duges*, in 1897 (F). Ca. 8 mi. W. of San Felipe, Cerro del Fraile, *Sohns* 452 (MICH, MO, US). PUEBLA: Mexique-Acatzingo, District de Tepeaca, *Nicolas*, July 7, 1909 (F). DISTRITO FEDERAL: C. de Progreso, *Matuda* 19676 (MICH). MICHOACÁN: Quinceo, *Arsène* 3218 (GH, ILL, MO, NY, US). Loma Santa María, *Arsène* 8581 (MO, US). Cerro San Miguel, *Arsène* 9937 (MO, US). Atzimba National Park, *Beetle* M–128 (US). Zacapu, *Hernández, Ruppert, & Guevara* X–2822 (US). 18 mi. E. of Morelia, *King & Soderstrom* 5011 (MEXU, MICH, SMU, TEX, US). 8–10 mi. NW. of C. Hidalgo, *McVaugh* 9925 (MICH, US). Pátzcuaro, *Seler* 1227 (GH, US). Quiroga, *Soderstrom* 552 (US), 555 (US); *Sohns* 806 (US). GUERRERO: Petlacala, *Mexia* 9098 (CAS, F, GH, MO, NY, UC, US). Between Ayusinapa and Petatlán, *Nelson* 2122 (US). "MICHOACÁN ET GUERRERO": El Canizal, *Langlassé* 750 (GH, US, isotypes of *M. meziana*). OAXACA: Río Grande (N. of Niltepec) to Finca "La Gloria," *Hernández & Sharp* X–1257 (US).

GUATEMALA: HUEHUETENANGO: 10 km. W. of Aguacatán, *Williams, Molina, & Williams* 21844 (US).

Muhlenbergia macrotis is distinguished by the prominent sheath auricles that attain a length of 1 cm. or more (as much as 10 cm. in *Hernández* X–4641!) and in the mostly glabrous and awnless or cuspidate lemmas. It is closely allied to *M. distichophylla* which has long auricles, but the lemmas bear a tiny tuft of hairs toward the base of the margins and are usually long-awned. The culms and panicles of *M. macrotis* are usually thicker and more robust than in *M. distichophylla*. Comparison may also be made with *M. robusta*, but that species has only rudimentary sheath auricles and the lemmas, although mostly glabrous, sometimes have sparse short hairs at the base.

Muhlenbergia macrotis was originally described by Piper in 1905 as an *Epicampes* from a specimen collected by Rose in Zacatecas, Mexico, in 1897. It was known only from the type collection. Hitchcock transferred *E. macrotis* to *Muhlenbergia* in 1935, at the same time he transferred *E. minutiflorus* to the genus naming the latter *M. meziana*.

Muhlenbergia meziana Hitchc. is considered as synonymous with *M. macrotis* in the present treatment. The original description of the former characterizes a specimen with very long auricles (to 45 mm.

in length), flat blades to 4 mm. in width, a dense panicle, and spikelets 2.5–2.75 mm. long.

The collection listed by Mez in his description of *Epicampes minutiflorus* is "E. Langlassé, bei El Canizal, Michoacán (Mexico)," without collection number. The specimen in the U.S. National Herbarium marked as the type is E. Langlassé, no. 750, El Canizal, Michoacán. This specimen, however, does not agree in all respects with the original description, for the auricles are less than 1 cm. long and the spikelets are 2–2.5 (averaging 2) mm. long. This leaves some doubt as to the collection Mez had in mind when he described *E. minutiflorus*. Nevertheless, the completely glabrous lemmas, the white, almost translucent glumes, and relatively long auricles place it with other specimens of *M. meziana*. The type appears, therefore, to be an aberrant representative of the species.

The holotype of *M. macrotis* agrees with *M. meziana*, with the exceptions that the spikelets are often a little longer and the florets exceed the glumes in length. The glumes, however, are 2–2.5 mm. long, rounded, almost translucent, and nerveless, like those of *M. meziana* specimens. Many of the spikelets in the panicle of the holotype of *M. macrotis* are diseased. I have noticed that in diseased panicles of other *Muhlenbergia* species the florets often become longer than normal, exceeding the glumes where the florets were normally contained within them. This perhaps explains why many of the florets are so long in the spikelets of the type specimen of *M. macrotis* which, in other respects, is similar to specimens of *M. meziana*. Specimens similar in general to the type collection of *Muhlenbergia meziana* occur in the same geographic region where the type of *M. macrotis* was found, and therefore it seems likely that the holotype of *M. macrotis* was only a diseased specimen of the species later described as *M. meziana*. The following list, a comparison of the major characters of specimens of *M. meziana* and the holotype of *M. macrotis*, illustrates the similarity.

	M. meziana	*M. macrotis*
height	125–230 cm.	134 cm.
culm surface	mostly glabrous	glabrous
node surface	glabrous to slightly pubescent	glabrous
sheath surface	glabrous	glabrous
upper throat	scabrous	scabrous
collar	glabrous to scaberulous	glabrous
blade width	2–6 (mostly 3–4) mm.	4–5 mm.
upper surface of blade	scaberulous to scabrous (mostly scabrous)	scaberulous
lower surface of blade	scabrous	scabrous
ligule length	3–13.5 (usually 5–8) mm.	11 mm.

	M. meziana	*M. macrotis*
auricle length	1–7 (usually about 3) cm.	to 3.5 and 4 cm.
panicle length	26–65 cm.	38 cm.
panicle width	1.5–6 cm.	1.5 cm.
panicle color	light green or whitish green	greenish tan (old panicle only)
axis surface	scaberulous to scabrous	scabrous
length of panicle branches:		
primary	5–11.8 cm.	7 cm.
secondary	1–4.5 cm.	2 cm.
tertiary	to ca. 1 cm.	lacking
spikelet length	2–3 mm.	2.5–3.6 mm.
glumes	equal, sometimes less than floret	equal, usually less than floret
glume length	2–3 mm.	2–2.5 mm.
glume surface	glabrous, nerveless or rarely obscurely 1-nerved	glabrous, nerveless
lemma length	1.8–2.3 mm.	ca. 3.2 mm.
lemma surface	glabrous	glabrous
awn length	usually lacking, lemma rarely cuspidate	lacking

8. Muhlenbergia distichophylla (J. S. Presl) Kunth. Rev. Gram. Supp. xvi. 1830.

Podosaemum distichophyllum J. S. Presl. Rel. Haenk. I: 231. 1830. (Mexico: without precise locality, *Haenke* 173).

Epicampes stricta var. *distichophylla* (J. S. Presl) Jones, Contr. West. Bot. 14:6. 1912. Based on *Podosaemum distichophyllum* J. S. Presl.

Muhlenbergia angustifolia Swallen. N. Amer. Fl. 17(6): 457. 1935. (Mexico: Jalisco, *Pringle* 2346).

Caespitose perennial; culms stout, glabrous, 1–1.75 m. tall; nodes 4, glabrous or somewhat puberulent beneath; basal sheaths compressed-keeled, mostly glabrous, sometimes scaberulous; ligule membranous throughout, entire at the base and lacerate above, or finely lacerate throughout, 4–8 mm. long, longer on the innovations; sheath auricles 4–8 (usually 6–8) mm. long, the auricles of the upper culm sheaths longer than those of the lower; blades of the culm to 90 cm. long, long-attenuate, becoming threadlike at the tip, flat or folded, 1.5–4.5 (mostly 2–2.5) mm. wide when unfolded, narrow in comparison with the sheaths from which they depart, the upper surface of the blade scaberulous to scabrous, lower surface scabrous, the edges of the blades minutely saw-toothed; upper throat scabrous; collar glabrous to scabrous (mostly scaberulous).

Panicle erect, somewhat lax at the tip, light green to tan (rarely purplish), the branches spreading widely, 35–60 cm. long, to 5 cm. or more in width; axis scaberulous to scabrous (mostly scabrous), the lower primary branches 6–13 cm. long, the secondary branches 1–6 cm. long, the tertiary branches 0.5–2 cm. long; pedicles of the lateral

spikelets 0.2–0.8 mm. long, those of the terminal spikelets to 2 mm., glabrous to scaberulous (usually scaberulous); spikelets 1.5–2.5 (usually 1.7–2) mm. long; glumes longer than the floret, the first glume often a little longer than the second, glabrous to scaberulous, broadly acute, awnless, hyaline, nerveless; lemma 1.4–2.5 (usually 1.7–2) mm. long, glabrous throughout except for a tuft of short hairs at the base of the margins, rounded at the tip, 3-nerved, the middle nerve becoming purplish and thickened toward the tip, excurrent as an awn 4–16 mm. (usually 1 cm. or more) in length; palea equal to or slightly shorter than the lemma, glabrous.

Fragment of type in the U.S. National Herbarium, collected in Mexico, without precise locality, by Haenke (no. 173).

DISTRIBUTION: Rocky hills and exposed areas of oak woods, at elevations of 1,500–7,500 ft., from Jalisco, Mexico, southeastward into Guatemala. Apparently infrequent.

MEXICO: *Haenke* 173 (US fragment of type of *Podosaemum distichophyllum*, ex W). JALISCO: Barranca de Oblatos, *Hitchcock* 7335 (NY, US). SW. of La Resolana, road to La Huerta, *McVaugh* 21106 (MICH, US). Above (N. of) La Cuesta, road to Talpa de Allende, *McVaugh* 21224 (MICH, US), 21225 (MICH, US). Guadalajara, *Pringle* 2346 (GH, NY, UC, US, isotypes of *M. angustifolia*). MEXICO: Tejupilco, Temascaltepec, *Hinton* 2719 (GH, LL, NY, US). Luvianos, Temascaltepec, *Hinton* 5302 (ARIZ, NY, US). Amatepec, *Matuda* 29874 (US), 29875 (US). "MICHOACAN ET GUERRERO": Sierra Madre, *Langlassé* 607 (GH, US). Cerro Mamegal, *Langlassé* 674 (GH, US). GUERRERO: Carboneras-Filo Mayor, *Hinton* 9910 (MICH, US). Vallecitos, *Hinton* 11635 (ARIZ, LL, MO, NY, US). 15 mi. N. of Tierra Colorada, *Reeder & Reeder* 4159 (US, YU). CHIAPAS: Escuintla, *Matuda* 319 (MICH, US). Mt. Ovando, *Matuda* 322 (MICH, MO, US).

GUATEMALA: HUEHUETENANGO: E. of San Sebastián, *Standley* 81480 (US). Near crossing of Río San Juan Ixtán, E. of San Rafael Pétzal, *Standley* 83016 (US). W. of Huehuetenango, *Williams, Molina, & Williams* 22309 (US).

Muhlenbergia distichophylla is distinguished by long sheath auricles and awned lemmas that are glabrous except for a small tuft of hairs on the margins toward the base. It is apparently most closely allied to *M. macrotis*, also possessing long sheath auricles, but lemmas that are awnless and entirely glabrous. Moreover, it has a denser panicle than *M. distichophylla* and a more robust habit. Label data for *M. distichophylla* indicates flowering from the end of November through May; *M. macrotis* blooms earlier.

Although *M. angustifolia* Swallen was recognized in North American Flora (1935) and has been maintained as distinct in the U.S. National Herbarium, it is represented only by specimens of the original collection of 1889. Additional collections of *M. distichophylla* have been made since the description of *M. angustifolia*, and a critical comparison of all specimens with the holotype of the latter revealed that the characters that distinguish it are not of sufficient importance for specific

recognition. The following comparison of the two illustrates this point.

	M. distichophylla specimens	*M. angustifolia* holotype
height	135–173 cm.	111–139 cm.
culm surface	glabrous	glabrous
node surface	glabrous or puberulent below	glabrous to puberulent below
sheath surface	usually glabrous	glabrous
upper throat	scabrous	scaberulous or scabrous
collar	scaberulous to scabrous (rarely glabrous)	glabrous
blade width	1.5–4.5 mm.	1.5–2 mm.
blade length	37–91 cm.	48 cm.
upper surface of blade	scaberulous to scabrous	glabrous or scaberulous
lower surface of blade	scabrous	scaberulous to scabrous
ligule texture	membranous, lacerate	membranous, lacerate
ligule length	4–8 mm., sometimes more	6–14 mm.
auricle length	0.2–4.5 cm.	1.7–3 cm.
panicle length	30–58 cm.	30–48 cm.
panicle width	usually 3.5–5 cm.	2–2.5 cm.
axis surface	scaberulous to scabrous (mostly scabrous)	scabrous
panicle color	greenish tan	light green
panicle branches:		
primary, length	6–12 cm.	4–6.5 cm.
secondary, length	1.6 cm.	1.5 cm.
tertiary, length	0.2 cm.	lacking
spikelet length	1.5–2.5 mm.	2.2–2.5 mm.
glume surface	glabrous	glabrous
lemma length	1.4–2 mm.	2.1–2.3 mm.
lemma surface	glabrous except for hairs toward the base of the margins (in both)	
awn of lemma, length	4.5–16 mm.	8–9 mm.

9. Muhlenbergia versicolor Swallen. Contr. U.S. Nat. Herb. 29: 412. 1950.

Muehlenbergia distichophylla var. *mutica* Scribn. ex Urbina. Cat. Pl. Mex. 393. 1897. Nomen nudum. Of the two collections listed, *Pringle*, 2360 = *M. macrotis*, and *Pringle* 5577 = *M. versicolor*.

Caespitose perennial; culms glabrous or somewhat puberulent, 82–199 (mostly 100–150) cm. tall; nodes 3 or 4, glabrous or pubescent below; basal sheaths compressed, but not strongly keeled, the old sheaths brown and somewhat fibrillose; ligule membranous throughout, 5–22 (usually more than 10) mm. long, usually flanked on either side by auricles that become membranous and twisted above, the firm, brown base of such auricles usually 4–8 mm. long; blades of the middle of the culm shorter than those of the lower part, 12–27 cm. long, usually folded, 2–5 mm. wide when flat; upper surface of the blade scaberulous to scabrous, the lower surface scabrous (lower surface usually scabrous and the upper surface scaberulous); upper throat scaberulous to scabrous; collar glabrous to puberulent.

Panicle erect, narrow, the branches ascending, lead green to purplish green, 17–60 (usually 20–40) cm. long, 1.5–6 cm. wide; axis scaberulous to scabrous; primary branches 4–11.5 cm., secondary branches 1.5–3.5 cm. long, tertiary branches lacking or to 0.5 cm. long, when present; pedicels of the lateral spikelets 1–2.5 mm. long, those of the terminal spikelets relatively long, to 3–5 mm., the pedicels glabrous on the lower part, becoming scaberulous on the thickened part below the spikelet; spikelets 2.5–3.5 (usually 3 or more, rarely to 4) mm. long; glumes usually a little shorter than the floret, the second glume longer than the first, the tips erose (under high power) or awn-tipped, the awns to 1.2 mm. long, frequently only the second glume awned and the first acute, usually scaberulous (rarely glabrous), hyaline, nerveless or faintly 1-nerved; lemmas acute, 2.5–3.5 (mostly about 3) mm. long, 3-nerved, villous over the lower half or two-thirds of the back on and between the nerves, and more densely so on the margins, awn 17–30 mm. long, flexuous; callus of lemma long-pilose; palea equaling or a little longer than the lemma, moderately to densely villous between and, sometimes, on the keels.

Holotype in the U.S. National Herbarium, no. 1961991, collected about 170 kilometers north of Oaxaca City, Oaxaca, Mexico, December 13, 1945, by Efraím Hernández Xolocotzi and J. A. Jenkins (no. X–810).

DISTRIBUTION: Rocky mountainsides and ledges, and slopes of barrancas. Rather uncommon, ranging in Mexico from Michoacán and the state of Mexico southeastward to Honduras.

MEXICO: GUANAJUATO: NE. of Cd. Guanajuato, *Reeder & Reeder* 3095 (YU. PUEBLA: Zapotitlán de las Salinas, SE. of Techuacán, *Hernández*, Oct. 27, 1960 (CHAP, US). Zapotitlán, near Tehuacán, *Ross*, Oct. 1906 (US). Between Apala and the top of Cerro Chichiltepec, *Smith, Peterson, & Tejeda* 3879 (US). MORELOS: Sierra de Ocuila rumbo Mexicapa, *Lyonnet* 2873 (US). Valle de Tepeite, *Lyonnet & Elcoro* 1838 (US). VERACRUZ: Maltrata, *Kerber* 226 (US). MEXICO: Rincón, Temascaltepec, *Hinton* 2081 (MO, NY, US). Socabón, Temascaltepec, *Hinton* 2324 (GH, LL, MICH, NY, US). Tejupilco, Temascaltepec, *Hinton* 2719 (GH). Sultepec, *Matuda* 26615 (US). Ixtaccihuatl, *Purpus* 1611 (ILL, MO, US). Salto de Agua, *Purpus* 1629 (US). 4 mi. S. of Tenancingo, *Reeder & Reeder* 4168 (US, YU). DISTRITO FEDERAL: Lomas de Tacubaya, *Gándara*, in 1938 (US). Villa Guerrero, *Tateoka* 1119 (US). MICHOACÁN: Lomas de la Huerta, *Arsène* 2465 (ILL, MO), 2465½ (F, US), 2825 (MO, NY, US), 5438 (NY, US), 5446 (ILL, MO, NY, UC, US), 5851 (MO, US), May 30, 1909 (US). Punguato, *Arsène* 2674 (US). Cerros de San Miguel, *Arsène* 5304 (NY, US), 6803 (US). Loma Santa Maria, *Arsène* 8585 (MO, US). Along road from Tsitzio-Tiquicheo-Huetamo-Altamira, *Sohns* 880 (US). GUERRERO: Teotepec, Mina, *Hinton* 14803 (ARIZ, ILL, LL, NY, TEX, US). OAXACA: Ca. 170 km. N. of Oaxaco City, *Hernández & Jenkins* X–810 (US holotype). Ixtlan de Juárez, *Krueger & Gillespie* 25 (CAS, LL, MO). Mina de Dolores, near Talea, *Liebmann* 673 (US fragment), 984, in 1841–43 (US). Mecoatlán, S. Andrés, *Liebmann* 736 (US fragment). Dolores, *Liebmann* 737 (MO, US). Reyes, *Nelson* 1780 (US).

(?)Sierra de San Felipe, *Pringle* 5576 (GH, MEXU, US), 5577 (US); (?)*Smith* 927 (in part) (MO, NY, US). Temascalapa to San Ildefonso de Villa Alta proper, *Santos* 3530 (NY, US). 45 mi. N. of Oaxaca, *Soderstrom* 417 (US). CHIAPAS: Between San Cristóbal Las Casas and San Gregorio, *Hernández & Sharp* 534 (US). Barranca Honda, Siltepec, *Matuda* 4124 (GH, LL, MICH, NY).

GUATEMALA: HUEHUETENANGO: Aguacatán road, 10 km. E. of Huehuetenango, *Standley* 82073 (F, US). Between San Sebastián H. and large peñasco above town, *Steyermark* 50504 (F, US). Barranco "Palo Negro" about 10 km. W. of Aguacatán, *Williams, Molina, & Williams* 21850 (US). SAN MARCOS: San Marcos, *Lehmann* 1578 (US fragment, ex G). SOLOLÁ: Lago Atitlán, *de Koninck* 146 (US).

HONDURAS: MORAZÁN: Suyapa, *Swallen* 11277 (US).

Muhlenbergia versicolor is distinguished by the long ligule and usually short sheath auricles, the narrow, densely flowered dark green or purplish-green panicles, the spikelets over 3 mm. long, the lemmas long-awned and villous over most of the surface on and between the nerves. It appears to be most closely related to *M. emersleyi*, and most herbarium specimens have been determined as that species. Although the two are similar in having long ligules and pubescence on the long-awned lemmas, they are easily separated. In *M. versicolor* almost the whole lemma is sparsely to densely villous on and between the nerves; in *M. emersleyi* the pubescence is confined to the midnerve and margins. The sheaths in *M. versicolor* are characterized usually by short auricles but these are lacking in *M. emersleyi*. The spikelet is dark green or purplish green in *M. versicolor*, but lighter and most often purplish or tan in *M. emersleyi*.

Specimens of *Epicampes* (*Smith* 927; *Pringle* 5576, 5577) collected on the summit ledges of Cerro de San Felipe (above the city of Oaxaca, at an elevation of about 10,000 ft.) are without doubt allied to *M. versicolor*. The base of the plant, the lead-green panicles, long spikelets, and villous lemmas are characteristics of *M. versicolor*. These specimens, however, exhibit some fundamental differences from the typical plants: The glumes are blunt rather than acute or dentate and awn-tipped as in *M. versicolor;* the auricles of the sheaths are very long, 1–3.5 cm., those of *M. versicolor* being less than 1 cm. long; the panicles are narrower, shorter, and the branches more appressed. In one specimen the lemmas are awnless, but long-awned in others, as in typical *M. versicolor*. When more information becomes available from additional field studies on Cerro de San Felipe, this curious group of specimens may prove to represent a distinct species.

10. Muhlenbergia gigantea (Fourn.) Hitchc. N. Amer. Fl. 17(6):461. 1935.
Epicampes expansa Fourn. Mex. Pl. 2:88. 1886. (*Botteri* 104 in part [*Botteri & Sumichrast* 104], Orizaba [Veracruz], Mexico. *Botteri* 104 in part is also cited by Fournier under *Epicampes mutica* Rupr. ex Fourn.)

Epicampes bourgaei Fourn. Mex. Pl. 2:88. 1886. (*Bourgeau* 2973, Escamela pr. Orizaba [Veracruz], Mexico.)

Epicampes bourgaei var. *mutica* Fourn. Mex. Pl. 2:88. 1886. (*Liebmann* 676, 678 Mirador [Veracruz], Mexico, and *Liebmann* 677, Tlaltengo [Veracruz], cited.)

Epicampes laxiuscula Fourn. Mex. Pl. 2:88. 1886. (*Botteri* 155, Orizaba [Veracruz], Mexico.)

Epicampes gigantea Fourn. Mex. Pl. 2:88. 1886. Basis of *Muhlenbergia gigantea* (Fourn.) Hitchc. (*Bourgeau* 3137, Río Blanco near Orizaba [Veracruz], Mexico.)

Epicampes ehrenbergii Mez. Repert. Sp. Nov. Fedde 17:212. 1921. (Type from Cuesta de Pinolco [Hidalgo?], Mexico.) This species was questionably referred to *Muhlenbergia robusta* (Fourn.) Hitchc. in N. Amer. Fl. 17(6):462. Although the type has not been seen, the description is that of *M. gigantea* for it states, in part: "ligulis magnis . . ." (the ligule of *M. robusta* is very short) and "Inflorescentia myriantha, bene thyrsoidea, 3 pinnatim panniculata [sic] . . ." (which must refer to the typically large and widely spreading panicle of *M. gigantea*).

Muhlenbergia alta Hitchc. N. Amer. Fl. 17(6):461. 1935. (*Hitchcock* 7180, Jalisco, Mexico.)

Muhlenbergia magna Hitchc. N. Amer. Fl. 17(6):460. 1935. (*Pringle* 3335, Jalisco, Mexico.)

Strongly caespitose perennial; culms stout and thick, robust, glabrous or somewhat scaberulous, 130–300 cm. (mostly 1.5–2.5 m.) tall; nodes 3, glabrous below; basal sheaths strongly compressed-keeled, glabrous or somewhat scaberulous; ligule membranous throughout, generally undivided at the base, becoming lacerate above, 1–3.5 (usually 1–1.5) cm. long; sheath auricles lacking, rarely rudimentary ones present; blades of the culm 35–115 (usually more than 65) cm. long, flat, the edges saw-toothed, 2.5–12 (usually 5–8) mm. wide, upper surface of the blade usually scaberulous, the lower surface scaberulous to scabrous, scabrous-ciliate on the margins near the ligule; upper throat scaberulous to scabrous; collar glabrous (sometimes scaberulous).

Panicle very large and open, the branches weak and lax and somewhat drooping or more rigidly flexuous, purplish or purplish brown, 45–110 (usually 50–100) cm. long, 20–30 cm. or wider, the branches opening wide, long-naked below, the aggregates of spikelets borne on the tertiary and quaternary branches, the groups of branches borne distant from each other on the axis; primary branches 11–27 (usually 15–20) cm. long, the secondary branches 1.5–12 (usually 4–10) cm. long, the tertiary branches 0.5–5.5 (usually 1–4) cm. long, quaternary branches, when present, to 2.5 cm. long; pedicels shorter than the spikelets, usually glabrous (sometimes scaberulous); spikelets 1.4–2.5 (mostly 1.5–2.2) mm. long; glumes rounded or acutish at the tip, about equal, a little longer than the floret, glabrous or scaberulous, awnless, 1-nerved; lemmas rounded or acutish at the tip, 1.3–2.2 (mostly 1.6–2)

mm. long, glabrous, 3-nerved, awnless (the midnerve sometimes becoming darker and thickened toward the tip and extending beyond it as a tiny point); palea equaling the lemma, glabrous.

Fragment of type in the U.S. National Herbarium, collected in region d'Orizaba, Río Blanco, Veracruz, Mexico, Sept. 30, 1866, by Bourgeau (no. 3137).

DISTRIBUTION: Open rocky slopes and barrancas, at elevations of 2,000–7,500 ft., most commonly found at ca. 3,500–5,000 ft. Known only from Mexico, ranging from Sinaloa and Durango southeastward to Chiapas. Apparently infrequent.

MEXICO: SINALOA: E. of Santa Lucía, *Reeder & Reeder* 2488 (YU). DURANGO: W. of La Ciudad (Mazatlán-Durango road), *Reeder & Reeder* 2522 (YU). JALISCO: SW. Autlán, *Hernández* 4643 (CHAP). Zapotlán, *Hitchcock* 7180 (US, holotype of *M. alta*), 7247 (ILL, US). Puente San Pedro, SW. of Tecalitlán *McVaugh* 18096 (MICH). Guadalajara, *Pringle* 3335 (F, GH, NY, UC, US, isotypes of *M. magna*), 11738 (CAS, F, GH, MO, US). Sierra Madre, W. of Bolaños, *Rose* 3002 (US). Guadalajara, *Soderstrom* 607 (US, YU). VERACRUZ: Orizaba, *Botteri* 103 (US fragment, ex CGE), 104 (US fragment of type of *E. expansa*, ex CGE), 159 (US fragment, ex CGE). Escamela, region d'Orizaba, *Bourgeau* 2973 (US fragment of type of *E. bourgaei*, ex P). Orizaba, Río Blanco, *Bourgeau* 3137 (US fragment of type of *E. gigantea*, ex LE, P). Orizaba, Cerro del Borrego, "*Curso de ecología vegetal*," Dec. 14, 1959 (CHAP). Mango de Dn. Bartolo carretera-Veracruz-Córdoba, *Hernández, Tapia, & Malthus* SE–1482 (CHAP). Mirador, *Liebmann* 676 (US), 678 (US). Orizaba, "*C. Mohr herbarium*" (US). Orizaba, *Müller*, in 1850 (NY). Veracruz a 22 km. de Catemaco sobre la carretera Acayucan, *Tapia & Martínez* SE–644 (CHAP). Loc.? *von Rozynski*, in 1932 (1933?) (F, NY, YU). MEXICO: Cajones, Temascaltepec, *Hinton* 2386 (MO, NY, US). Vigas, Temascaltepec, *Hinton* 2626 (MO, NY, US). MICHOACÁN: Pto. Cruces, Coalcoman, *Hinton* 12471 (ARIZ, GH, LL, MO, NY, TEX, US). 22 km. S. of Uruapan, *King & Soderstrom* 4860 (MEXU, MICH, SMU, TEX, US). Between Charapengo and El Guaco on road from Uruapan to Apatzingán, *Moore, Hernández & Porras* 5750 (UC, US). GUERRERO: Machón, Mina, *Hinton* 9635 (MO, NY, US). 13 mi. N. of Tierra Colorada, *Reeder & Reeder* 4157 (US, YU). OAXACA: Cerro de San Felipe, *Conzatti* 710 (GH), *Conzatti* 2534 (US). Tepenixtlahuaca, distrito de Tuquila, *Conzatti* 4376 (GH, US). Reyes, *Nelson* 1779 (GH, US). Temascalapa to San Ildefonso de Villa Alta, district of Villa Alta, *Santos* 3531 (US). CHIAPAS: between San Geronimo and El Pozo via Abasolo and El Retiro, *Hernández & Sharp* X–597 (US). Tuxtla Gutiérrez, *Tateoka* 1103 (US).

Muhlenbergia gigantea is distinguished by its large size, robust culms, long ligule, large, wide-spreading panicles, and relatively small glabrous spikelets. It is most closely related to *M. mutica* and the type specimens of both are from Orizaba, Veracruz, Mexico. The spikelets differ in the ratio of glume length to floret length: In *M. gigantea* the glumes are about equal to the floret; in *M. mutica* the glumes exceed the floret by several millimeters. In the latter species

the glumes are very acute, but more rounded or acutish in the former. This is possibly a variation within the same species, for the terminal spikelets of *M. gigantea* rarely have elongated glumes extending beyond the floret for several millimeters. An example is found in the type material of *M. gigantea* (*Bourgeau* 3137). The spikelets average 2 mm. in length, but in one case the terminal spikelet is 2.5 mm., enclosing a 1.5 mm. floret. As relatively few collections of *M. mutica* have been made, I do not feel safe in generalizing on the variability of the species at this time, and for this reason am not combining them. Additional field work, particularly in the region of Orizaba, Veracruz, will be necessary before this problem can be solved.

Herbarium specimens of *M. robusta* are often confused with *M. gigantea*. When only a panicle is present, the wide-spreading habit is often not obvious in dried condition. If vegetative parts are present, the short ligule and rudimentary sheath auricles of *M. robusta* readily separate it from *M. gigantea*.

Hitchcock (1935) described two new species from Jalisco, Mexico: *Muhlenbergia magna* (*Pringle* 3335) and *M. alta* (*Hitchcock* 7180). These specimens, like *M. gigantea*, are large robust plants with long lacerate ligules, wide-spreading panicles, and glabrous spikelets. *Muhlenbergia alta* is described as differing from *M. gigantea* in its smaller spikelets, 1.5 mm., as opposed to 2–2.5 mm. A study of the holotype of *M. alta* reveals that the spikelets actually range from 1.5–2 mm. in length but such variability also occurs in specimens referred to *M. gigantea!* The holotype of *M. magna* exhibits no basic differences from *M. gigantea* except for the more rigid and erect panicle branches. Color of the panicle is the only character used in the key to separate the two species (purplish in *M. gigantea*, brownish in *M. magna*). Many of the specimens available for study could not be placed satisfactorily on the basis of erectness versus laxness of panicle branches or on the color of the inflorescence. A striking example of color difference was found in specimens collected in Durango, Mexico (*J. & C. Reeder* 2522, yellowish brown) and Sinaloa, Mexico (*J. & C. Reeder* 2488, dark purple). Both plants are similar except for color. The label of the former reads: "On a steep rocky slope. Both yellow and purple forms here."

Within limits, characters such as spikelet size and panicle color and habit are variable in species of *Epicampes* and are not of specific magnitude. As *M. magna* and *M. alta* appear to represent nothing more than normal variation within *M. gigantea*, they are here combined. The following comparison of characters of these three supposed species illustrates their similarity:

	M. gigantea specimens	*M. alta* holotype	*M. magna* holotype
height	160–300 cm.	193 cm.	172 cm.
culm surface	glabrous	glabrous	glabrous
node surface	glabrous	glabrous	glabrous
basal sheaths	glabrous, compressed-keeled	glabrous compressed-keeled	glabrous compressed-keeled
upper throat	scaberulous to scabrous	scaberulous	scaberulous
collar	mostly glabrous (sometimes scaberulous)	glabrous	glabrous
blade width	4–12 (usually 7–9) mm.	6–9 mm.	3.5 (in other specimens 2.5–7) mm.
upper surface of blade	glabrous to scaberulous (mostly scaberulous)	scaberulous	glabrous to scaberulous
ligule texture	membranous, becoming lacerate	membranous, becoming lacerate	membranous, lacerate
ligule length	5–35 mm. (usually 1 cm. or more)	6 mm.	ca. 10 mm.
sheath auricles	lacking	lacking	lacking
panicle length	45–110 cm.	100 cm.	46 cm.
panicle width	20–35 cm. or more, widely spreading	over 30 cm.	25 cm.
axis surface	scaberulous	scaberulous	glabrous to scaberulous
pedicel length	0.2–0.8 mm., less than spikelet	less than spikelet	0.4–0.7 mm., less than spikelet
pedicel surface	glabrous to scaberulous	glabrous	scaberulous
panicle color	purplish (sometimes brownish)	dark purple	brownish
panicle branches:			
primary	12–27 cm.	25 cm.	14 cm.
secondary	4–12 cm.	11 cm.	5.5 cm.
tertiary	1–5.5 cm.	2 cm.	1.5 cm.
quaternary	to 2.5 cm.	—	—
glume 1st/2nd	about equal	equal	equal
glume surface	glabrous to scaberulous	scaberulous	glabrous
spikelet length	1.4–2.5 mm.	1.5–2 mm.	1.7–2 mm.
lemma length	1.3–2.2 mm.	1.3 mm.	1.6 mm.
lemma surface	glabrous	glabrous	glabrous
awn length of lemma	awnless or extending from midnerve as a tiny point	awnless	awnless or extending from midnerve as a tiny point

11. Muhlenbergia mutica (Rupr. ex Fourn.) Hitchc. N. Amer. Fl. 17(6):459. 1935.

Epicampes mutica Ruprecht. Bull. Acad. Roy. Sci. Bruxelles, Belg. IX(2): 230. 1842. Nomen nudum. (*Galeotti* 5797, savanes de Mirador, Zacuapan, et Cantaranas près du Puente Nacional, Veracruz, Mexico.)

Epicampes mutica Rupr. ex Fourn. Mex. Pl. 2:87. 1886.

Strongly caespitose, robust perennial; culms stout, thick, glabrous, 2 meters or more tall; nodes 3, glabrous below; basal sheaths strongly compressed-keeled, glabrous; ligule membranous, undivided at the base, lacerate above, about 1 cm. long; sheath auricles lacking; blades of the culm 35 cm. long (in specimen examined), 4–5 mm. wide, the upper and lower surfaces of the blades scaberulous to scabrous; upper throat scaberulous; collar glabrous.

Panicle very large and open, the branches weak and lax, brownish or purplish brown, about 1 m. long and 30 cm. or wider; the primary branches as much as 30 cm. long, the secondary branches 6–12 cm. long, the tertiary branches 1.5–2 cm. long, quaternary branches lacking; axis scaberulous; pedicels shorter than the spikelet, those of the terminal spikelets longer than those of the lateral ones, scaberulous, becoming more scabrous just beneath the spikelet; spikelets 2.1–3.1 (mostly 2.5–2.8) mm. long; glumes about equal, much longer than the floret, scaberulous, acute, awnless, nerveless or indistinctly 1-nerved; lemmas 1.9–2.2 mm. long, glabrous, roundish at the tip, obscurely 3-nerved, awnless; palea a little shorter than the lemma, glabrous.

Fragment of type (ex P) in the U.S. National Herbarium, collected in "savanes de Mirador, Zacuapan, et Cantaranas près du Puente Nacional, Veracruz, México," by Galeotti (no. 5797). This specimen was cited by Ruprecht in 1842 without description. In his description of the species, Fournier (Mex. Pl. 2:87. 1886) cited this specimen, along with several other syntypes. *Galeotti* 5797 (P) is here designated as the lectotype.

DISTRIBUTION: Open rocky hillsides, at elevations of about 4,000–6,300 ft. Known only from Mexico in the states of Veracruz and Chiapas. Apparently rare.

MEXICO: VERACRUZ: Orizaba, *Botteri* 111 (US fragment, ex P), 729 (US fragment); *Botteri & Sumichrast* 104 (US fragment, ex P); *Hitchcock* 6348 (US). Mirador, Zacuapan, and Cantaranas, *Galeotti* 5797 (US fragment of lectotype, ex P). CHIAPAS: El Pozo to Oxchuc, *Hernández & Sharp* X–616 (US).

Muhlenbergia mutica is distinguished by its nonauriculate sheaths, large, wide-spreading panicle, and acute glumes much longer than the floret. It is most closely related to and doubtfully distinct from *M. gigantea*. The only character to separate the two is the length of the glumes in relation to the floret: In *M. gigantea* the glumes equal the floret, but in *M. mutica* the floret is exceeded by the glumes. Until

more material is available to study this character critically, I prefer not to combine the two species.

12. Muhlenbergia inaequalis Soderstrom, sp. nov.

Perennis caespitosa, culmis angustis erectis glabris vel scaberulis 50–70 cm. altis, nodis 3–4 glabris, vaginis inferioribus compressis et carinatis; ligula membranacea-firma, 0.5–1.5 mm. longa; laminis culmi angustis attenuatisque conduplicatis vel planis utrinque scaberulis, ca. 15–26 cm. longis, 2–3 mm. latis; collis glabris; panicula laxa, 25–30 cm. longa, usque ad 10 cm. lata, axe scaberulo, ramis primariis usque ad 8 cm. longis, secundariis usque ad 3 cm. longis, pedicellis scaberulis; spiculis 2.5–3.1 (plerumque 3) mm. longis, glumis acutis, inaequalibus, quam flosculo brevioribus, glabris, nervis 0 vel 1, indistinctis, lemmatibus acutis, 2.5–3(3) mm. longis, inferne brevi-pilosis, infra apicem aristatis, aristis 1–2 cm. longis.

A *M. emersleyi* Vasey ligulis brevioribus, glumis inaequalibus quam flosculo brevioribus, et lemmatibus inferne brevi-pilosis differt.

Caespitose perennial; culms erect, narrow, glabrous to scaberulous about ½–¾ m. tall; nodes 3–4, glabrous; basal sheaths compressed-keeled, glabrous to scaberulous; ligule a short, brown, firm membranous rim 0.5–1.5 mm. long; sheath auricles lacking; blades of the culm 15–26 cm. long, 2–3 mm. wide, flat or folded, the upper and lower surfaces scaberulous; upper throat scaberulous; collar glabrous.

Panicle pyramidal, lax above, the branches loosely ascending or spreading, purplish to purplish tan, 25–30 cm. long, 5–10 cm. wide; axis scaberulous; branches naked below, the lower primary branches of the panicle 5–8 cm. long, the secondary branches 2–3 cm. long; pedicels scaberulous, those of the lateral spikelets 0.5–1.8 (1–1.2) mm. long, those of the terminal spikelets longer; spikelets 2.5–3.1 (mostly 3) mm. long; glumes acute and some awn-tipped, unequal and shorter than the floret, the first about three-fourths as long as, and narrower than, the second, 1.6–2.5 (1.9) mm. long, the second 2–3 (2.4–2.5) mm. long, glabrous or scaberulous, nerveless or indistinctly 1-nerved; lemmas acute, 2.5–3(3) mm. long, short-pilose over the lower part and especially on the midnerve one-half to three-fourths its length, the lemma 3-nerved, the middle nerve excurrent from below the tip as a flexuous awn 1–2 cm. long; palea about equaling the lemma, short-pilose between the keels for one-half to three-fourths its length; anthers yellow, 1.1–1.2 mm. long.

Holotype in the U.S. National Herbarium, no. 2380325, collected in Quebrada de Durí, Estado de Trujillo, Venezuela, November 11, 1939, by A. Müller (no. 973). Isotypes at VEN.

DISTRIBUTION: Mountains to the south and southwest of Lago de Maracaibo, in Venezuela and Colombia.

VENEZUELA: Trujillo: Quebrada de Durí, *Müller* 973 (US holotype, VEN isotypes). Mérida: *Funck & Schlim* 1017 (US fragment ex Herb. Boissier).
COLOMBIA: (?) *Mutisi* 1760–1808 (US fragment ex MA). Norte de Santander: Ocaña *Schlim* 190 (US fragments ex Herb. Boissier and K).

Muhlenbergia inaequalis has the habit of *M. emersleyi* and possesses features of other species closely related to that species. The pyramidal panicle of long-awned spikelets looks much like typical *M. emersleyi* but the spikelets differ in important respects. The glumes are unequal and shorter than the floret, as in *M. scoparia.* The lemma is short-pilose over the lower part, on and between the nerves, somewhat as in *M. versicolor.* The ligule is a short, membranous rim as in *M. breviligula.* The short ligule, unequal glumes shorter than the lemma, and pubescence on and between the nerves of the lemma readily distinguish this species.

The collection of José Celestino Mutis, 1760–1808, is represented in the U.S. National Herbarium by only a panicle. Tentatively it is assigned to this species, as the glumes are unequal and shorter than the floret. However, the glumes are broader and more scabrous and less acute than those of the type and the panicle is more compact. The lemmas are short-pilose like those of the type, but shorter. The spikelets of the Schlim, and Funck and Schlim collections match closely those of the type specimen.

The name "inaequalis" refers to the very unequal glumes, an unusual feature in *Epicampes.*

13. Muhlenbergia scoparia Vasey. Contr. U.S. Nat. Herb. 1:283. 1893.

Muhlenbergia carinata Mez. Repert. Sp. Nov. Fedde 17:213. 1921. (Based on *Pringle* 2350, which is also the lectotype of *Muhlenbergia scoparia* Vasey [1893].)

Caespitose perennial; culms 55–88 (usually about 75) cm. tall, glabrous to scaberulous; nodes glabrous, covered by the sheaths; basal sheaths compressed-keeled, glabrous, becoming scaberulous toward the collar, the old sheaths and blades at the base curled, generally reddish-brown, fibrillose; ligule membranous throughout, usually hidden between the folded blade above, 8–16 (usually 10 or more) mm. long; sheath auricles lacking; blades of the culm 25–50 (mostly about 50) cm. long, flat or folded, 1–4.5 mm. wide when flat (mostly 2.5–3 mm. wide), the edges of the blade slightly saw-toothed, upper and lower surfaces of the blade scaberulous to scabrous; upper throat scabrous; collar glabrous to scaberulous (mostly scaberulous).

Panicle loose, nodding, the branches narrow, borne in groups at intervals along the axis, light green to purplish or brownish green, 22–30 cm. long, 1.5–5 cm. wide; axis scaberulous to very scabrous, strongly ribbed; primary branches 3.5–14 (mostly 4–9) cm. long,

naked below, the secondary branches 1–5.5 cm. long, tertiary branches lacking or, when present, 1–2 cm. long; pedicels of the lateral spikelets 0.6–1.2 mm. long, those of the terminal spikelets to 3 mm. long, scaberulous scabrous, especially below the spikelet; spikelets 1.5–2.2 (averaging 2) mm. long, excluding the awn tips; glumes very acute, first glume shorter than the second, awn-tipped (especially the second), the awn sometimes as much as 1 mm. long, glumes glabrous to scabrous, hyaline, nerveless or indistinctly 1-nerved; lemmas 1–2 (usually 1.5–2) mm. long, exceeding the glumes by a few mm., glabrous or scaberulous dorsally, the lower margins of the lemma conspicuously short-pilose, bearing short straight hairs to one-third the length of the lemma; lemmas acutish at the tip, 3-nerved, awned from just below the tip, the awn 6–15 mm. long; palea a little shorter than the lemma, glabrous.

Lectotype in the U.S. National Herbarium, no. 999089, collected on rocky hills near Guadalajara, Jalisco, Mexico, Nov. 10, 1889, by C. G. Pringle (no. 2350).

Vasey cited two specimens in the original description and remarked, "collected at Batopilas by Dr. Edward Palmer in 1885, and at Guadalajara (No. 2350) by C. G. Pringle in 1889." Of these syntypes, Hitchcock (1935b, p. 457) cited the latter as the type, thus effectively choosing it as lectotype. A note by Dr. Agnes Chase on the sheet of *Pringle* 2350 reads "second of the 2 specimens cited, but first is incomplete, description of habit, height, leaves, etc. must have been drawn from this."

DISTRIBUTION: Exposed rocky mountainsides and open areas in the oak zone, at elevations of 2,500–6,000 ft. Mexico, from Chihuahua, Sonora, and Sinaloa, south to Michoacán. Apparently infrequent.

MEXICO: *Palmer*, in 1886 (DS, ILL, NY). SONORA: Canyon Sapopa, Río Mayo, *Gentry* 1289 (GH, MO). Sierra Tecurahui, *Barclay & Arguelles* 19387 (US). CHIHUAHUA: Batopilas, *Palmer*, in 1885 (ARIZ, US, isosyntypes). SINALOA: Mesa Malqueson, Cerro Colorado, *Gentry* 5178 (ARIZ, F, GH, MO, NY, UC). Loc.? *Ortega* 1120 (F, US). 10 mi. E. of Santa Lucía (road from Villa Union to Durango), *Reeder & Reeder* 2451 (YU). NAYARIT: La Barranca, *Jones* 23446 (CAS, GH, MO, UC), Feb. 21, 1927 (NY, POM). Mina Esperanza, Rosa Morada, *Ortega* 6672 (CAS, US), Acaponeta, *Rose*, Aug. 2, 1897 (US). JALISCO: Km. 211 Guadalajara to Barra de Navidad *Aquilera* in 1958 (CHAP). 3 mi. N. of Pihaumo, *McVaugh & Koelz* 1394 (MICH, US). San Sebastián, trail to Monte Oscuro, Sierra Madre Mountains, *Mexia* 1644 (CAS, DS, F, GH, MICH, MO, NY, UC, US). Guadalajara, *Pringle* 2350 (F, LL, MEXU, US, isolectotypes). MICHOACÁN: Coalcomán, *Hinton* 12699 (ARIZ, GH, LL, MO, NY, TEX, US).

Muhlenbergia scoparia is distinguished by its unequal, awn-tipped glumes that are shorter than the floret. It is probably most closely related to *M. grandis*, sharing the features of reddish-brown basal

sheaths, short spikelets, and long-awned, comparatively glabrous lemmas with a short pilose callus. In *M. grandis*, however, the glumes are about equal, not awn-tipped, and the ligule is shorter, usually no more than 6 mm. Both species have a range farther west in Mexico than the majority of species of *Epicampes*, occurring in the states of Sinaloa, Nayarit, and Jalisco. *Muhlenbergia scoparia* also has a more extensive north-south range, from Chihuahua and Sonora to Michoacán.

14. Muhlenbergia iridifolia Soderstrom, sp. nov.

Perennis caespitosa, culmis erectis glabris 1¼ m. altis, nodis 4 glabris, vaginis inferioribus forte compressis et carinatis; ligula membranacea-firma, 5–7 mm. longa; laminis culmi latis acutisque conduplicatis vel planis utrinque glabris, 30–70 cm. longis, 4–7 mm. latis; callis glabris; panicula supra laxa, 45 cm. longa, 3 cm. lata, axe glabro, ramis primariis 7–8 cm. longis, secundariis ca. 3 cm. longis, pedicellis glabris; spiculis 4–4.2 mm. longis, glumis angustis minute aristatis, quam flosculo paulo longioribus, glabris, nervis 0 vel 1, indistinctis, lemmatibus angustis, 4 mm. longis, 3-nervis, glabris, inferne brevipilosis, infra apicem aristatis, aristis 2–2.5 cm. longis.

Caespitose perennial; culms erect, glabrous, about 1¼ m. tall; nodes 4, glabrous; basal sheaths strongly compressed-keeled, glabrous, spreading outward in a distinct flabellate fashion; ligule brown, firm-membranous, lacerate but rather blunt or truncate, conspicuous from side view, 5–7 mm. long; sheath auricles lacking; blades of the culm 30–70 cm. long, 4–7 mm. wide, the older blades folded but younger blades mostly flat, the upper and lower surfaces glabrous except for the scabrous, saw-toothed margins and midnerve on the undersurface; upper throat glabrous; collar glabrous.

Panicle lax above, the branches loosely ascending or spreading, purple, 45 cm. long, 3 cm. wide; axis completely glabrous; branches naked below, the lower primary branches of the panicle 7–8 cm. long, the secondary branches about 3 cm. long; pedicels glabrous, the swollen portion just beneath the spikelet puberulent, mostly 1–2 mm. long, those of the terminal spikelets longer and more variable in length; spikelets 4–4.2 mm. long; glumes purple, narrow, acute, minutely awn-tipped, the second a little longer than the first, just exceeding the floret, glabrous, nerveless or indistinctly 1-nerved; lemmas narrow, acute, about 4 mm. long, glabrous, short-pilose at juncture of lemma and callus at the base on palea side, the hairs about one-fourth the length of lemma, 3-nerved, the middle nerve excurrent from just below the tip as a slightly flexuous purple awn 2–2.5 cm. long; palea a little shorter than lemma, completely glabrous.

Holotype in the University of Michigan herbarium, collected in Jalisco, Mexico, in "Steep mountains 11–12 miles south of Talpa de Allende, in the headwaters of a west branch of Río de Talpa; barranca above a rapid clear stream, in dense forest of *Quercus, Carpinus, Distylium, Magnolia, Podocarpus,* with pine forest on the ridges above; abundant in the pine forest; in clumps, inflorescence purple; alt. 1200–1700 m., 23–25 November 1960," by Rogers McVaugh (no. 21313). Isotype at US. Known only from the type collection.

Although I would prefer to have additional collections at hand in describing this new species, there is little doubt that it is distinct. The habit of the inflorescence and spikelets with awn-tipped glumes and lemmas glabrous except for the short-pilose base, suggest a relationship with *M. scoparia.* The distinct fan-shaped appearance of sheaths and the stiff, rather wide, flat blades ascending erectly much like an iris suggested the name "iridifolia." The firm brown ligules are conspicuous and appear to be chopped off, leaving a firm brown base about 5–7 mm. long. The combination of long spikelets (4 mm.), awn-tipped glumes, and lemmas glabrous except at the base where the callus is short-pilose, readily distinguishes this species from all others in *Epicampes.*

15. Muhlenbergia speciosa Vasey. Bull. Torrey Club 13 (12):231. 1886.

Bealia speciosa (Vasey) Beal. Grasses N. Amer. 2:268. 1896. Based on *Muhlenbergia speciosa* Vasey.

Epicampes speciosa (Vasey) Jones. Contr. West. Bot. 14:7. 1912. Based on *Muhlenbergia speciosa* Vasey.

Caespitose perennial; culms pubescent or villous, the pubescence present as broad bands on the culm, glabrous between the bands, 95–129 cm. tall; nodes 5, densely pubescent to villous below and usually above; basal sheaths compressed-keeled, glabrous below and becoming villous toward the collar, or villous throughout, especially along the edges; ligule a membranous rim, 0.3–1.1 mm. long; sheath auricles lacking; blades of culm 36–52 cm. long, 2.5–4 mm. wide when flat, the blades usually folded with the edges rolled backward on the lower (abaxial) surface, upper surface of the blade villous (or scabrous) at the base near the ligule, the pubescence becoming sparse toward the distal end, here the surface scaberulous, or scaberulous with scattered long hairs, the lower surface of blade generally more villous than the upper surface and for the greater part of its length, especially villous near the ligule, becoming less so distally, here the surface scabrous; upper throat densely villous.

Panicle large and plumose, the branches ascending or opening outward, whitish or purplish white, 41–62 cm. long, 5–11 cm. wide; axis glabrous to scabrous with scattered long hairs; lower primary branches 9–13 cm. long, naked below; secondary branches 3.5–5 cm. long,

naked below; tertiary branches 1.3–3 cm. long; quaternary branches, when present, to 0.8 cm. long; pedicels of the lateral spikelets 0.5–2 mm. long, of the terminal spikelets relatively long, 1.5–5.5 mm., glabrous to scaberulous, often with scattered long hairs on the surface; spikelets 1.2–2.2 (averaging less than 2) mm. long; glumes equal or the second a little longer than the first, 1.4–2.3 mm. long, usually a little longer than the floret, mostly villous, rounded or lobed at the tip or rarely with an awn tip, hyaline, nerveless, white; lemmas 1.2–2.2 mm. long, villous throughout, especially on the lateral margins, 3-nerved, the nerves purple and become thickened toward the tip, awn of the lemma to 17 mm. long; callus of the lemma short and densely pilose; palea obtuse, a little shorter than the lemma, villous, especially between the keels.

Type in the U.S. National Herbarium, no. 999062, collected in "southwestern Chihuahua, Mexico," August to November 1885, by Dr. Edward Palmer (no. 30). Isotypes at GH and MEXU.

DISTRIBUTION: Found only in Mexico, where it is confined to rocky slopes in the pine-oak zone and in arroyos, at elevations of about 1,000–6,600 ft. From southwestern Chihuahua through western Durango, Sinaloa, Nayarit, and into Jalisco. Apparently infrequent.

MEXICO: *Palmer*, in 1886 (TAES). CHIHUAHUA: *Palmer* 30, Aug. to Nov. 1885 (US holotype, GH, MEXU, isotypes). SINALOA: Culiacán, Cofradía, *Brandegee*, Oct. 26, 1904 (POM, UC, US). Palmito and vicinity along Durango-Sinaloa highway, *Gentry & Arguelles* 18201 (LL, US). Santa Lucía, *Mexia* 490 (CAS, MO, UC, US). DURANGO: La Bajada, Tamazula, *Ortega* 4335 (US). 21 mi. E. of Santa Lucía, *Reeder & Reeder* 2476, aff. *M. speciosa* (YU). NAYARIT: Tepic, *Jones* 23438 (CAS, GH), Feb. 10, 1927 (NY). 9 mi. N. of Compostela, *McVaugh & Koelz* 575 (MICH). Ca. 5.5 mi. SW. of Jalisco, road to El Malinal, *McVaugh & Koelz* 668 (MICH). "Along banks of arroyos," *Palmer* 1919, in 1892 (GH, MO, NY, US). 7 mi. NW. of Tepic, *Reeder & Reeder* 4210 (US, YU), 4211 (US, YU). JALISCO: SW. Autlán, *Hernández* 4638 (CHAP, US). 4 mi. N.-NE. of Talpa de Allende, *McVaugh* 20102 (MICH, US). Ca. 8 mi. SW. of La Resolana, *McVaugh* 21105 (MICH, US). 3–5 road mi. above (N. of) La Cuesta, road to Talpa de Allende, *McVaugh* 21226 (MICH, US).

Muhlenbergia speciosa is distinguished by the more or less villous sheaths, blades, and culms, the very short ligule (about 1 mm. or less), a large plumose panicle, and small spikelets (mostly less than 2 mm. long), the lemmas long-awned. It appears to be most closely related to *M. pubescens*. Both species are generally villous throughout, the ligule is relatively short, and the glumes, lemmas, and paleas are more or less villous. *Muhlenbergia pubescens* differs in the longer ligule (2–3 mm.), a denser panicle with larger spikelets (mostly 2.4–2.6 mm.), and the shorter awns of the lemmas. The ranges of both overlap in southwestern Chihuahua and western Durango, Mexico, and some hybridization may possibly occur. One specimen, *Reeder & Reeder* 2476, from western Durango, seems to be somewhat intermediate

between these two species and perhaps represents such a hybrid. The long spreading branches of the panicle in this specimen and the very short ligule are characters of *M. speciosa*. The 2.5 mm. long spikelets and the short-awned lemmas are features of *M. pubescens*. The habit and overall appearance are those of *M. speciosa*, to which it appears to be more closely allied. The extent of such putative hybrids cannot be determined until many more collections are made in this region. Comparison may also be made with *M. grandis* which is similar in habit and occupies a similar range. Unlike *M. speciosa* it has glabrous culms, foliage, and glumes, and longer ligule (1.5–6 mm.)

16. Muhlenbergia pubescens (H.B.K.) Hitchc. N. Amer. Fl. 17(6):460. 1935, as to type, not as to description (see *M. distans* Swallen).

Agrostis pubescens H.B.K. Nov. Gen. & Sp. I:136. 1815. Basis of *Muhlenbergia pubescens* (H.B.K.) Hitchc. (Type collected in "scopulosis juxta Villalpando, Santa Rosa, et Cerro del Cubilete," 7800–8760 ft. [mining areas around the city of Guanajuato, Guanajuato, Mexico].)

Agrostis lanata H.B.K. Nov. Gen. & Sp. I:136. 1815. (Type from same localities as preceding.)

Cinna? *pubescens* (H.B.K.) Kunth. Rev. Gram. 1:67. 1829. Based on *Agrostis pubescens* H.B.K.

Cinna? *lanata* (H.B.K.) Kunth. Rev. Gram. 1:67. 1829. Based on *Agrostis lanata* H.B.K.

Epicampes pubescens (H.B.K.) Presl ex Kunth. Enum. Pl. 1:209. 1833. Based on *Agrostis pubescens* H.B.K.

Epicampes lanata (H.B.K.) Presl ex Kunth. Enum. Pl. 1:209. 1833. Based on *Agrostis lanata* H.B.K.

Epicampes pubescens (H.B.K.) Jones. Contr. West. Bot. 14:7. 1912. Based on *Agrostis pubescens* H.B.K.

Muhlenbergia lanata (H.B.K.) Hitchc. N. Amer. Fl. 17(6):459. 1935. Based on *Agrostis lanata* H.B.K.

Caespitose perennial; culms erect, 57–154 (usually about 100–125) cm. tall, sparsely to densely villous, especially on the lower part; nodes 3–4, sparsely to densely villous, especially below; basal sheaths compressed-keeled, villous (rarely scabrous with long sparse hairs); collar villous or scabrous with sparse long hairs; ligule membranous, usually finely lacerated, 1.5–6 (usually 2–4) mm. long; sheath auricles lacking; blades 12–61 (usually 25–50) cm. long, usually short on the upper part of the culm, 2.5–6.5 (usually 3–4) mm. wide, flat or folded, upper surface villous at base, becoming less villous toward the tip (rarely only scabrous with long scattered hairs), upper surface villous throughout or sometimes scabrous with long scattered hairs; blades of the culm constricted and villous at point of attachment to sheath; upper throat villous.

Panicle erect, columnar, densely flowered, gray or purplish gray, 12–49 (usually 20–40) cm. long, 2–7 (usually 3–7) cm. wide, the branches of the panicle ascending, floriferous to base; axis villous, rarely sparsely so; primary branches 3–11.5 (usually 5–8) cm. long,

secondary branches 1–5 (usually 1–2) cm. long, tertiary branches rarely to 1.5 cm. long; pedicels shorter than the spikelets, villous (sometimes sparsely so), 0.3–1 mm. long; spikelets 2.5–3 mm. long; glumes broadly acute at the tip, longer than the floret, almost equal or the first 1–2 mm. shorter than the second, sparsely to densely villous, nerveless, gray, often purplish at the base; lemma 2.2–3 (usually 2.4–2.6) mm. long, sparsely to densely villous throughout except at tip, 3-nerved, the median nerve often extending as an awn from just below the tip, 1–10 (usually 6–7) mm. long, straight or somewhat flexuous; palea villous throughout, rarely sparsely so.

Fragment of panicle of possible type marked "*Agrostis pubescens*" (in Kunth's script) in the U.S. National Herbarium, ex Herb. Humboldt & Bonpland (P), collected near Guanajuato, Guanajuato, Mexico, "in scopulosis juxta Villalpando, Santa Rosa, et Cerro del Cubilete," 7800–8760 ft. A photograph of the specimen is with the fragment.

DISTRIBUTION: Common on rocky mountain slopes and ledges and in rocky ravines, canyons, and barrancas, at elevations of about 5,600–8,000 ft. Known only from Mexico, from Chihuahua and Durango south to Puebla. A collection from Oaxaca is doubtfuly referred to this species.

MEXICO: CHIHUAHUA: Hills near Chihuahua, *Pringle* 391 (F, GH, MO, US), 983 (MEXU, NY). 37 mi. S. of Villa Matamoros, *Reeder, Reeder, & Soderstrom* 3451 (US, YU). DURANGO: Canyon Cantero, Sierra de Gamón, *Gentry* 8406 (GH, MEXU, MICH, UC, US). 40 km. S. of Durango, *Hernández, Ruppert, & Guevara* X–2561 (US). 20 km. S. of Durango, *Hernández, Ruppert, & Guevara* X–2576 (US). Km. 1395, Carretera Juárez, Parral-La Zarca, *Hernández & Tapia* N–589 (CHAP). Durango, *Hitchcock* 7587 (ILL, US), 7652 (NY, US). SW. of Durango on Durango-Mazatlán road, *Soderstrom* 763 (US, YU), 768 (US, YU), 769 (US, YU), 773 (US, YU), 774 (US, YU). N. of Durango on Durango-Juárez road, *Soderstrom* 788 (US, YU). 23 mi. W. of Durango, *Reeder & Reeder* 2548 (YU), 2592 (YU). 31 mi. W. of Cd. Durango, *Reeder & Reeder* 2578 (YU), 2590 (YU). 6 mi. W. of Navíos, *Reeder, Reeder, & Soderstrom* 3377 (US, YU), 3411 (US, YU), 3412 (US, YU), 3413 (US, YU), 3414 (US, YU). Sierra Madre Occidental, W. of Cd. Durango, *Reeder, Reeder, & Soderstrom* 3428 (US, YU). 3 mi. E. of Navíos, *Reeder, Reeder, & Soderstrom* 3429 (US, YU), 3430 (US, YU). 5 mi. E. of Navíos, *Reeder, Reeder, & Soderstrom* 3433 (US, YU), 3434 (US, YU), 3435 (US, YU). 11 mi. W. of Durango, *Reeder, Reeder, & Soderstrom* 3444 (US, YU). ZACATECAS: 2 mi. W. of Sombrerete, *Soderstrom* 733 (US). SAN LUIS POTOSÍ: 22° N. Lat., *Parry & Palmer* 933 (F, GH, MO, US). 20 mi. SW. of San Luis Potosí, *Reeder, Reeder, & Soderstrom* 3304 (US, YU). *Schaffner* 190 (US). "Ex convalli S. L. P.," *Schaffner*, in 1876 (GH). San Francisco in the Sierra de San Miguelito, *Sohns* 1049 (US). Canyon del Lobo, Sierra de San Miguelito, *Sohns* 1158 (US). Canyon del Muerto, Sierra de San Miguelito, *Sohns* 1319 (US), 1327 (US). AGUASCALIENTES: 7 mi. E. of Ojo Caliente, *Reeder & Reeder* 4193 (US, YU). Mountains above Presa Calles, *Shreve* 9258 (ARIZ, US). JALISCO: San Juan de los Lagos, *Hernández* X–4608 (CHAP, US). Ojuelos-Aquascalientes, *Hernández, Ruppert, & Guevara* X–2513

(US), X–2515 (US). Road to León, Gto., 5 mi. SE. of junction at Lagos de Moreno, *McVaugh* 17800 (MICH). 7 mi. SE. of Lagos de Moreno, *Reeder & Reeder* 2306 (YU). 15 mi. SE. from Encarnación de Díaz on highway 45 to Lagos de Moreno, *Soderstrom* 692 (US), 693 (US), 694 (US), 696 (US), 698 (US). GUANAJUATO: About 9 mi. from Guanajuato, *Moore* 1355 (GH, MICH, UC, US). 695 (US), 12 mi. E. of Guanajuato, *Reeder & Reeder* 3088 (YU). 13 mi. NE. of Guanajuato, *Reeder & Reeder* 3093 (YU). 2–4 km. E. of Guanajuato, *Sohns* 298 (US). About 6 km. E. of Guanajuato, *Sohns* 302 (US), 313 (US). About 8 km. W. of San Felipe, *Sohns* 433. PUEBLA: 5 mi. NE. of Zacatepec, *Soderstrom* 483 (US, YU). TLAXCALA: Santa Ana Chiautempan, *Arsène* 1715 (GH, MO, NY, US). MEXICO: About 45 mi. S. of San Juan del Río, *Reeder & Reeder* 2235 (YU). El Pedregal, just S. of Mexico, City *Reeder & Reeder* 3047 (YU). OAXACA: (?)27 mi. NW. of Cd. Oaxaca, *Reeder & Reeder* 2184, aff. *M. pubescens* (YU).

Muhlenbergia pubescens appears to be most closely related to *M. speciosa* and like that species has moderately to densely villous vegetative parts, a relatively short ligule, and blades usually constricted at the base. It is distinguished from *M. speciosa* by the denser panicles with the branches more appressed, longer spikelets (usually 2.4–2.6 mm. in contrast to 2 mm.), and shorter awns on the lemmas (7 mm. or less as opposed to 10 mm. or more).

In 1815 Kunth described two species of *Agrostis*, *A. pubescens* and *A. lanata*, and indicated that the latter might be a variety of the former. *Agrostis pubescens* was described as 3–4 ft. tall, generally glabrous throughout, pubescent under the nodes, having a short, lacerate ligule, white, nerveless, punctate-scabrous glumes, and lemmas pubescent at the base. *Agrostis lanata* was described as 3 ft. or taller, generally lanate throughout, having pubescent nodes, a short, lacerate ligule, and pilose glumes, lemmas, and paleas.

Presl (1830), along with his description of the original species of *Epicampes*, mentioned that these two species of *Agrostis* probably belonged with his new genus and added that *A. lanata* might be a variety of *A. pubescens*, but he made no transfers. Kunth (1833), following the opinion of Presl, formally transferred them to *Epicampes*. Jones (1912), commenting on *E. pubescens*, stated: "This is *Agrostis pubescens* H.B.K. . . . *A. lanata* is a synonym." He is the only author who stated, without reservation, that they are clearly synonymous and are not worthy of recognition as varieties within one species. Hitchcock (1935) transferred *E. pubescens* and *E. lanatus* to *Muhlenbergia* and, following the lead of Kunth and Presl, indicated that *M. lanata* might be a variety of *M. pubescens*.

Muhlenbergia lanata, as based upon *Agrostis lanata*, refers to a widespread plant characterized by villous lemmas, a very short ligule (about 3 mm. long), and moderately to densely villous glumes, culms, and sheaths. *Muhlenbergia pubescens*, as circumscribed by Hitchcock, is characterized by lemmas pubescent over the lower half,

a ligule 5–10 mm. long (or a little longer), and relatively glabrous glumes, culms, and sheaths.

The type collections of "*A. pubescens*" and "*A. lanata*" are from the same locality, near the city of Guanajuato. The majority of specimens from this area of Mexico are quite villous throughout, although occasionally the pubescence is confined mostly to the lemma, appearing more sparsely on the glumes and remainder of the plant. According to the original description these plants with sparse pubescence would be referred to "*A. pubescens.*" The very short ligule, short blades, and at least some pubescence on the other vegetative parts seem to indicate a less pubescent form than "*A. lanata,*" but certainly not a distinct species.

A fragment of a specimen marked *Agrostis pubescens*, in Kunth's handwriting (Mn. 5225, from the H.B.K. herbarium, P), and accompanying photograph in the U.S. National Herbarium are those of "*A. lanata*" of the original description. An annotation on the same sheet by Dr. Agnes Chase, dated 1935,[12] reads: "No specimen named '*A. lanata*' by Kunth has been found and no other named '*A. pubescens.*' " This fragment is mentioned above as the possible type of *Agrostis pubescens*, but the spikelets have villous rather than punctate-scabrous glumes as *A. pubescens* should have from the description, and so it is likely that this specimen is actually the type of *A. lanata,* and that the type of *A. pubescens* has not been found.

From the descriptions of Kunth, the amount of pubescence on the plant separated "*Agrostis pubescens*" from "*A. lanata.*" The former was described as mostly glabrous except below the nodes and the lemmas as pubescent toward the base; the latter as having pubescent basal sheaths, nodes, and spikelets.

A large number of specimens of both types were collected by the author and Prof. and Mrs. J. R. Reeder in the autumn of 1960 in central Mexico. Specimens referable to both "species" were collected near each other, in addition to specimens intermediate in amount of pubescence between the two. This leaves little doubt that the amount of pubescence is a variable character in these species and that both types are representatives of one species, *M. pubescens.* Special reference is made to the following comparison of specimens, showing extreme and intermediate types of pubescence. All specimens were collected in the same locality, 6 miles west of Navíos, Durango, Mexico.

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[12] In 1935, Dr. Agnes Chase, of the United States National Herbarium, critically studied and made notes on type specimens of grasses in many European herbaria.

Reeder, Reeder, & Soderstrom number	*Pubescence of sheaths*	*Pubescence of culm*	*Pubescence of blades*	*Ligule*	*Glumes*	*Lemma*	*Axis of panicle*	*Fits original description of Agrostis*
3411	only at base	sparsely pubescent; very pubescent around nodes	scabrous and with sparse long hairs	3 mm.	scaberulous only	villous on lower half	scabrous, not villous	*pubescens*
3412	villous	glabrous or with sparse long hairs: densely pubescent below nodes	villous	2 mm.	villous	villous through-out	lightly villous	*lanata*
3413	villous	glabrous or sparsely hairy, densely pubescent below nodes	sparsely villous	2 mm.	villous	villous on lower half	scabrous	*lanata*
3414	scabrous, some sparse pubescence	glabrous below, becoming densely pubescent below nodes	scabrous	3 mm.	sparse hairs	sparsely pubes-cent below	scabrous	*pubescens*

When correctly understood, *M. pubescens* embraces short to medium-sized plants, the ligule is short (about 3 mm.), the usually short blades of the culm are constricted and villous at the base, and the lemma is pubescent on and between the nerves. The basal sheaths, blades, and other parts are often densely villous, but the amount varies and is often restricted to the lower part of the basal sheaths or as sparse hairs over the various parts. Hitchcock (1935) misinterpreted *M. pubescens;* the plants he described have relatively long ligules, glabrous vegetative parts, relatively long brownish spikelets, and awnless or short-awned lemmas pubescent over the lower part, on and between the nerves. Such specimens appear to belong properly to *M. distans.* The two species, as treated in this work, may be distinguished as follows:

	M. pubescens	*M. distans*
spikelets	about 2–3 mm. long, white to purplish	averaging 3 mm. long
glumes	sparsely to densely villous, obtusish	glaucous, with roughed surface, acute
lemma	usually densely pubescent throughout	pubescent over lower part
ligule	usually 2–3 mm. long, membranous throughout	5–10 mm. long, firmer and browner at base than above
blades of culm	constricted and villous at at base	not constricted and villous at base
nodes	pubescent below	glabrous to scaberulous below; rarely pubescent
basal sheaths	villous, or at least slightly pubescent, with scattered long hairs	glabrous to scaberulous

17. Muhlenbergia robusta (Fourn.) Hitchc. N. Amer. Fl. 17(6):462. 1935.

Epicampes strictus J. S. Presl. Rel. Haenk. 1:235. 1830. Basis of *Muhlenbergia presliana* Hitchc. (Mexico: without precise locality, *Haenke*). Not *M. stricta* (Presl) Kunth. 1833.

Epicampes berlandieri Fourn. Mex. Pl. 2:89. 1886. Basis of *Muhlenbergia fournieriana* Hitchc. (Mexico: without precise locality, *Berlandier* 670). Not *M. berlandieri* Trin. 1841.

Epicampes robusta Fourn. Mex. Pl. 2:89. 1886. Basis of *Muhlenbergia robusta* (Fourn.) Hitchc. Fournier cites the following specimens in the original description:

Bourgeau 683, supra Tacubaya (state of Mexico). He also cites this collection under *Epicampes stricta* Presl (p. 89). Hemsley (1885) likewise cites it under *E. stricta* Presl. The lemmas are pubescent over the lower half and from a study of a fragment it appears to be *Muhlenbergia distans.*

Bourgeau 1153, Santa Fée, vallée de Mexico. A complete specimen ex P is in the U.S. National Herbarium. The lemmas are glabrous except for a few minute hairs at the base. Fragments in an envelope labeled *Bourgeau* 1153 ex LE consist of two elements. In one, probably *M. distans,* the lemmas are pubescent on the lower half and are awned. The other has

awnless lemmas but is pubescent on the lower midnerve and margins. Neither of these can be *Bourgeau* 1153.

Hahn 420, Cuernavaca, [Morelos], Mexico. Not seen.

Muhlenbergia fournieriana Hitchc. Journ. Washington Acad. Sci. 23:453. 1933. Based on *Epicampes berlandieri* Fourn.

Muhlenbergia presliana Hitchc. N. Amer. Fl. 17(6):462. 1935. Based on *Epicampes strictus* Presl.

Strongly caespitose perennial; culms stout, thick, erect, glabrous, 1–3 meters tall; nodes usually 4, glabrous below, the nodes covered by the sheaths; basal sheaths strongly compressed-keeled, glabrous (rarely scaberulous); ligule short, membranous, finely lacerated into narrow strands and hairs, 1.5–5 (usually 2–4) mm. long, longer on the innovations; rudimentary sheath auricles present, 1.5–5 (mostly 2–4.5) mm. long, rarely lacking or more than 5 mm. long; blades about 25–50 (mostly 30–50) cm. long, 3.5–6 (usually 4–5) mm. wide, the upper and lower surface scabrous, usually strongly so, the edges of the blades sharply saw-toothed; upper throat scabrous; collar glabrous, rarely scaberulous.

Panicle large, densely flowered, erect, purplish or greenish gray, columnar before anthesis, the branches spreading at flowering and becoming appressed at seed-set, 30–60 (usually 40–60) cm. long, rarely as much as 70–80 cm. long, 2–4 cm. wide (on herbarium specimen, much wider in field), the branches of the panicle naked below or floriferous to the base; axis thick, angled, scaberulous or scabrous; primary branches 4.5–17 (usually 5–8) cm. long, the secondary branches 1.3–6 (usually 1.5–3) cm. long, the tertiary branches 0.7–2.5 (usually 1 or less) cm. long; pedicels scaberulous or scabrous, those of the lateral spikelets very short, less than 1 mm. long, of the terminal spikelets a little longer; spikelets about 1.8–3.3 (mostly 2.1–2.8) mm. long, rarely longer; glumes acute to obtuse at the tip, equaling each other or the second a little longer than the first, glabrous to even scaberulous, purplish or greenish gray, longer than the floret, 1-nerved, often indistinctly so; lemma acutish, glabrous or evenly scaberulous, at most a few hairs at the base of the midnerve and margins, 3-nerved, the median nerve often extending into a rudimentary awn from just below the tip, usually less than 1 mm. long; callus of lemma glabrous or with only a few hairs; palea a little shorter than the lemma, glabrous or, at most, a few hairs between the keels toward the base.

Isolectotype in the U.S. National Herbarium, no. 999036, collected in "Barranca près Santa Fée, vallée de Mexico," Oct. 3, 1865, by E. Bourgeau (no. 1153).

Fournier cited three specimens in the original description. Of these Hitchcock (1935b, p. 462) cited *Bourgeau* 1153 as the type, and thus this is the lectotype.

DISTRIBUTION: Steep rocky mountainsides, slopes of canyons and barrancas, and eroded areas, at elevations of 3,000–7,000 ft., occurring most frequently at 5,000–6,000 ft. The most common species of *Epicampes* in southern Mexico, extending from Nayarit and Jalisco to Chiapas and into Guatemala and Nicaragua.

MEXICO: *Berlandier* 670 (US fragments of type of *E. berlandieri*, ex LE, P, W). *Haenke* (US fragment of type of *E. strictus*). *Palmer*, in 1884 (DS, NY, US). "Near river bank," *Schumann* 1754 (US). NAYARIT: SE. of Tepic, *McVaugh* 13393 (MEXU, SMU, US). JALISCO: Entre Pequeros y Tepatitlán, *Hernández* 4609 (CHAP). Zapotlán, *Hitchcock* 7172 (US), 7173 (US). Barranca de Oblatos, *Hitchcock* 7335 (ILL, NY). La Barranca, *Jones* 27658 (MO). N. of Autlán, *McVaugh* 19698 (MICH, US). SW. of Autlán, *McVaugh* 19899 (MICH, US). Río Blanco, *Palmer* 518, in 1886 (GH, MEXU, MO, NY, US). Guadalajara, *Pringle* 2321 (F, GH, MO, NY, UC, US), 11746 (CAS, F, GH, MO, US). 18 mi. S. of Guadalajara, *Reeder & Reeder* 2343 (YU). 3 mi W. of Tequila, *Reeder & Reeder* 4206 (US, YU). Sierra Madre, W. of Bolaños, *Rose* 2997 (GH, US). Ciudad Granja, W. of Guadalajara, *Soderstrom* 643 (US), 644 (US). SE. of Guadalajara, on road to Aquascalientes, *Soderstrom* 653 (US), 654 (US). 6 mi. E. of Santa Cruz, *Soderstrom* 566 (US), 567 (US), 568 (US), 569 (US), 570 (US), 571 (US), 572 (US). W. of Guadalajara on road to Tepic, *Soderstrom* 603 (US), 606 (US), 634 (US), 635 (US). 8 mi. E. of Guadalajara, near Barranca de Oblatos, *Soderstrom* 678 (US), 679 (US), 680 (US). GUANAJUATO: Guanajuato, *Kenoyer* 1765 (*M. robusta* X *M. emersleyi*?) (GH). 11 mi. NE. of Guanajuato, *Reeder & Reeder* 3081, aff. *M. robusta* (YU). 2–4 km. E. of Guanajuato, *Sohns* 297 (*M. robusta*?) (MICH). VERACRUZ: Orizaba, *Müller* 2130 (US). PUEBLA: Cerro Chiquihuite, *Arsène* 115 (US). PUEBLA: Cerro et fort de Guadalupe, *Arsène* 1186 (US). Mayorazgo, *Arsène* 1275 (MO, US). Cholula, *Arsène & Nicolas* 5441 (US); *Nicolas*, Sept. 15, 1910 (F). Rancho Posada near Puebla, *Nicolas* 303 (US). Esperanza, *Nicolas*, Sept. 8, 1909 (NY). Acatzingo, *Nicolas*, in 1909 (US). La Venta, *Sharp* 441664 (US). 6 mi. E. of Puebla, *Soderstrom* 387 (US), 388 (US), 389 (US), 390 (US). Zacatepec, *Soderstrom* 484 (US), 485 (US). MORELOS: Tautepec, *Gándara*, in 1935 (US). Atlatlahucan, *Gándara* (US). Teposteco, *Lyonnet* 2553 (US). Sierra de Ocuila rumbo Mexicapa, *Lyonnet* 2872 (US). Casa de Tepoztero, *Seler* 4320 (GH). MEXICO: Santa Fe (as Santa Fée), *Bourgeau* 1153 (US lectotype, fragments ex LE, P). Carboneras, Temascaltepec, *Hinton* 1853 (GH, NY). Rincón del Carmen, Temascaltepec, *Hinton* 1959 (MO, NY, US). Temascaltepec, Temascaltepec, *Hinton* 2053 (LL, MO, NY, US). Anonas, Temascaltepec, *Hinton* 2591 (CAS, LL, MICH, MO, NY, US). Sultepec, Sultepec, *Hinton* 3219 (NY). Luvianos, Temascaltepec, *Hinton* 5302 (NY). Tenango, *Matuda* 18846 (US). Guajimalpa to Río Hondo, *Matuda* 21811 (US). Valle de Bravo, *Matuda* 27232 (MO). Carretera México-Cuautla, *Ortega & Vázquez*, Oct. 12, 1960 (CHAP). 5 mi. N. of Tenancingo, *Reeder & Reeder* 4173 (US, YU). Santa Fe, *Rose & Painter* 8009 (US). 3 mi. NW. of Tlamanalco, *Soderstrom* 380 (US), 382 (US). DISTRITO FEDERAL: Chalco region, *Collins*, Oct. 4, 1921 (US). Pedregal, *Hitchcock* 5939 (SMU, US). Near Chapultepec Castle, *Hitchcock* 7839 (US). ¼ mi. S. of La Cima R.R. Station, *Iltis, Koeppen, & Iltis* 146 (US, WIS). Pedregal de San Angel, *Juzepczuk* 216 (US); *Lyonnet* 1670 (US); *Matuda* 19479 (US). Churubusco, *Orcutt* 4317 (GH, US). Coyoacán, *Ortega & Vázquez*, Oct. 9, 1960 (CHAP). Lava fields above the Valley of México, *Pringle* 9077 (GH, MO, US). El Pedregal, *Reeder & Reeder* 3053 (YU). Huipulco, *Rzedowski* 1350 (IPN). Between Ixtle and El Conejo,

Rzedowski 1929 (IPN). Eslava, *Rzedowski* 1999 (US). Sobre el Ixtle, *Rzedowski*, Dec. 21, 1952 (IPN). About 5 km. W. of San Andrés, *Sohns* 183 (US). Pedregal, *St. Pierre* 804 (MICH, US), 805 (MICH, US). Dolores, *St. Pierre* 869 (US). Ciudad Universitaria, *Tateoka* 1106 (US). MICHOACÁN: Lomas de la Huerta, *Arsène* 2628 (ILL, MO, NY, US), Oct 15, 1909 (GH). Barranca NW. de Punguato, *Arsène* 2673 (ILL, MO, NY, US), 3145 (ILL, NY, TEX, US), Oct. 18, 1909 (GH). Loma Santa María, *Arsène*, Sept. 2, 1909 (US). Zitácuaro-Coyota, *Hinton* 13409 (DS, GH, NY, US). 5 mi. N. of Cotija and 22 mi. S. of Jiquilpan, *King & Soderstrom* 4648 (MICH, SMU, TEX, US). 22 mi. S. of Uruapan, *King & Soderstrom* 4859 (MICH, US). Below Tecambaro on road to Chipio, *Moore, Hernández, & Porras* 5616 (UC, US). Between Mil Cumbres and Ciudad Hidalgo, *Moore, Hernández, & Porras* 5774 (US). Road from Lorelia to Toluca, *Reeder, Reeder, & Goodding* 1476 (YU). Zacapú, *Ruppert & Guevara* X–2830 (US). 3 mi. E. of Morelia, *Soderstrom* 544 (US), 545 (US), 545a (US). Quiroga, *Soderstrom* 552 (US), 553 (US). Uruapan to Nueva Italia, *Sohns* 865 (US). OAXACA: Oaxaca, *Hitchcock* 6141 (US), 6154 (US). Reyes, *Nelson* 1778 (GH, US). 27 mi. NW. of Cd. Oaxaca, *Reeder & Reeder* 2183 (YU). Huajuapan de León, *Soderstrom* 412 (US). Loc.?, *Tateoka* 1107 (US). CHIAPAS: Km. 1134, *Baldwin* 14345 (US). 15 mi. S. of Comitán, *Reeder & Reeder* 2096 (YU). 20 mi. E. of Chiapa de Corzo, *Reeder & Reeder* 2128 (YU).

GUATEMALA: HUEHUETENANGO: Huehuetenango, *Melhus & Goodman* 3562 (F). 10 km. W. of Aguacatán, *Williams, Molina, & Williams* 21848 (US). QUEZALTENANGO: Aguascalientes, *Seler* 3236 (GH). GUATEMALA: *Aguilar* 311 (F). Guatemala City, *Hitchcock* 9035 (CAS, US), 9063 ½ (US). Eureka, *Hitchcock* 9081 (MICH, US). Between Antigua and Guatemala City, *Hitchcock* 9146 (US). N. of Guatemala City, *Popenoe* 738 (US). SACATEPÉQUEZ: Santa María, *Hitchcock* 9129 (US). Antigua, *Standley* 61698 (F, US). CHIMALTENANGO: Alameda, *Johnston* 976 (F). Finca La Alameda, near Chimaltenango, *Standley* 59136 (F, US). SE. of Patzúm, *Standley* 61596 (F, US). Finca La Almeda, near Chimaltenango, *Standley* 79806 (F), 79729 (F). SOLOLÁ: Cerca del Lago Atitlán, *de Koninck* 145 (US). SANTA ROSA: Naranjo, *Heyde & Lux* 3932 (GH, MO, NY, US).

NICARAGUA: *Garnier* 1953 (GH, US). MANAGUA: Sierra de Managua, *Garnier*, "about 1930–1940" (F).

Muhlenbergia robusta is distinguished by its robust habit, very short fimbriate ligule, rudimentary sheath auricles, and awnless or short-awned, mostly glabrous, lemmas. Its closest relative appears to be *M. virletii*, which has a longer ligule (4–8 mm. rather than 2–4 mm.), rudimentary sheath auricles lacking, longer spikelets (mostly 3.5–3.6 mm. as opposed to 2.1–2.8 mm.), and the lemmas pubescent toward the base of the margins. The sheath auricles, short ligule, glabrous lemmas, and robust habit of *M. macrotis* also suggest a close relationship with *M. robusta*.

Muhlenbergia robusta is the dominant species of *Epicampes* found on rocky mountainsides in southern Mexico and might be thought of as the counterpart of *M. emersleyi* Vasey which is dominant in northern Mexico and southwestern United States. As in the latter species, *M. robusta* varies widely and some of the extreme forms have been described as species. Hitchcock (1935b) recognized two species, *M.*

robusta and *M. presliana*, the latter based on the type of *Epicampes*, *E. strictus* Presl.

The present study indicates that *M. presliana* and *M. robusta* are members of one polymorphic species. A comparison of characters from Hitchcock's descriptions discloses that the major distinction between the two species is spikelet size; in *M. robusta* it is 2.5–3 mm. long and only 2 mm. in *M. presliana*. Spikelet size is a variable character in all species of *Epicampes*. Within the *M. robusta* complex the spikelets vary in size from 1.8–3.3 mm., although usually 2.1–2.8 mm. long. The spikelets of a fragment of the type of *M. presliana* are mostly 2 mm. long, a few are 2.3 mm. Specimens with spikelets 2 mm. long are similar to specimens of *M. robusta* with longer spikelets and exhibit no other characters to delimit them as a distinct species.

In addition to variations of spikelet size and glume surface, the branches of the panicle are naked at the base in some specimens and in others floriferous to the base. Specimens exhibiting various combinations of these characters and intergrading forms have been found. Nevertheless, all possess the robust habit, relatively glabrous lemmas, short fimbriate ligule, and characteristic rudimentary sheath auricles generally about 3 mm. in length. In view of the lack of correlation of characters, it seems more realistic to regard *M. robusta* and *M. presliana* as members of a single variable species.

A rather unusual specimen, *Kenoyer* 1765 (Guanajuato, Mexico), may possibly be a hybrid between *M. robusta* and *M. emersleyi*. The Gray Herbarium specimen, the only one I have seen, has an incomplete culm and complete inflorescence. The latter is about 45 cm. long with ascending branches. The ligule is short-lacerate and small auricles are present, as in *M. robusta*, and the panicle is typical of that species. Although the shape and appearance of the spikelets are of that species, the lemmas are awned and slightly pubescent, in the pattern of *M. emersleyi*.

18. Muhlenbergia virletii (Fourn.) Soderstrom, comb. nov.

Epicampes virletii Fourn. Mex. Pl. 2:88. 1886. (*Virlet* 1415, San Luis de Potosí, Mexico)

Caespitose perennial; culms stout, erect, glabrous to scaberulous, about 1 m. tall; basal sheaths strongly compressed-keeled, glabrous to finely scaberulous; ligule membranous, lacerate above, 4–12 (usually 4–8) mm. long; sheath auricles lacking; blades of the culm folded, about 30–40 cm. long, 2.5–6 (usually 2.5–3.5) mm. wide, the upper and lower surfaces scabrous, the margins sharply saw-toothed; upper throat scabrous; collar scaberulous.

Panicle erect, dark green, 29–55 (usually 30–50) cm. long, 1.5–4 (usually 2–4) cm. wide, the branches ascending or spreading, naked

below, the spikelets clustered above; axis scabrous, primary branches 6–16.5 cm. long, secondary branches 2.5–5.5 cm. long; tertiary branches 1–1.5 cm. long; pedicels shorter than the spikelets, 0.7–2 mm. long, scabrous; spikelets 3–4 (mostly 3.5–3.6) mm. long; glumes equal to or longer than the floret, usually equal to each other, or the second glume 1–2 mm. longer than the first, green-translucent, often punctate-roughened, acute at tip, indistinctly 1-nerved; lemmas acuminate, 2.7–3.8 mm. long, sparsely to densely pubescent on the lower margins, glabrous dorsally (rarely a few sparse hairs on the midnerve below), 3-nerved, awnless or the awns rudimentary, no more than 0.5 mm. long; callus of lemma pilose; palea shorter than the lemma, glabrous or with a few hairs between the nerves.

Fragments of panicle of type, ex P–CO and Fournier herbarium (P) in the U.S. National Herbarium, no. 73225, collected in "Mexique, Prov. de San Luis," in 1851, by Virlet d'Aoust (no. 1415).

DISTRIBUTION: Arroyos and rocky hillsides in the pine-oak zone, at elevations of about 6,600–8,400 ft. Infrequent from San Luis Potosí in central Mexico, south to Puebla. A single collection from Durango is doubtfully referred to this species.

MEXICO: DURANGO: Km. 143 Durango-Mazatlán, *Hernández & Tapia* N–849 (*M. virletii* vel aff.) (CHAP). SAN LUIS POTOSÍ: *Virlet* 1415 (US fragment of type, ex P). PUEBLA: Manzanilla, *Arsène* 1693 (GH, ILL, MO, NY, US). Km. 47, camino de Puebla, *Matuda* 18611 (US). MORELOS: Lagunas Zempoala, *Lyonnet* 2515 (US). MEXICO: Comunidad, Temascaltepec, *Hinton* 2439 (MICH, NY, US). Sultepec, Sultepec, *Hinton* 3219 (ILL, MO, NY, US). 23 mi. SE. of México on highway 190, *Pratt* 751 (TEX). Near Santa Fe, *Rose & Painter* 8010 (NY, US). E. of Ixtlahuaca, *Soderstrom* 512 (US). DISTRITO FEDERAL: Desierto de Leones, *Matuda* 25930 (US). Cerca del Xitle, *Rzedowski* 2167 (IPN). Western part of the Pedregal, *Rzedowski* 2242 (US). Eslava, *St. Pierre* 813 (US). MICHOACÁN: Quinceo, *Arsène* 3201 (ILL, MO, NY, US). Morelia, *Arsène* 6999 (US). Ca. 18 mi. S. of Pátzcuaro, *King & Soderstrom* 5200 (US).

Muhlenbergia virletii is distinguished by the very long green spikelets, the lemmas glabrous except toward the base of the margins, the medium ligule, and the absence of sheath auricles. In its nearest ally, *M. robusta*, rudimentary sheath auricles are usually present, the spikelets are shorter, the lemmas are mostly glabrous throughout, and the ligule is shorter (mostly 2–4 mm. as opposed to 4–8 mm. long). The glumes of *M. robusta* are generally purplish or ashy gray; those of *M. virletii* are dark green and appear translucent.

Glume surface is more or less glabrous in some specimens, in others scaberulous or scabrous. Specimens collected in the same locality exhibit such differences. In spikelets of specimens previously referred to *M. presliana* the glumes are glabrous, although Hitchcock described them as scabrous. Specimens have been cited, however, with spikelets about 2 mm. long and the glumes scabrous, e.g., *Hitchcock* 9129

(Guatemala), *Gándara* (Morelos, Mexico), and *Moore, Hernández, & Porras* 5616 (Michoacán, Mexico). Furthermore, specimens were found with the glumes glabrous and the spikelets similar to those of the type of *E. strictus*, except larger, 2.5–3 mm. long, e.g., *Rzedowski* 1999 (México, D. F.). *Sohns* 183 (México, D. F.) has spikelets similar to those of *Rzedowski* 1999 but the glumes are scabrous.

19. Muhlenbergia breviligula Hitchc. N. Amer. Fl. 17(6):458. 1935.

Strongly caespitose perennial; culms stout, glabrous to scaberulous, 75–141 cm. tall; nodes 3, glabrous or slightly puberulent below, sometimes puberulent above the nodes; basal sheaths compressed-keeled, the old basal sheaths persistent, becoming brown, curled and fibrillose; ligule of the culm leaves a membranous rim of hairs 0.1–2 mm. long (usually negligible, less than 1 mm. long) those of the innovations sometimes over 1 cm. long; sheath auricles lacking or rudimentary, whitish, 1.5–6 mm. long when present; blades of the culm flat or folded 24–47 cm. long 2–3 (mostly 2.5) mm. wide when flat, the upper surface glabrous to scaberulous, the lower surface scaberulous to scabrous; upper throat scabrous, often pubescent; collar scabrous or puberulent.

Panicle nodding, rather dense, yellowish to purplish brown or purplish green, the branches ascending or opening outward, 30–51 (mostly 30–40) cm. long, 3–9 (mostly 3–5) cm. wide; axis scabrous, the primary branches 6–12 cm. long, the secondary branches 1.5–7 cm. long, the tertiary branches 0.5–3.5 cm. long; pedicels of the lateral spikelets 0.5–1.5 mm. long, those of the terminal spikelets to 3 mm. in length, scaberulous on the lower part, becoming scabrous just below the spikelet; spikelets 2–3 mm. long or sometimes longer (mostly 2.5–3 mm.); glumes about equal, equaling or a little longer than the floret, glabrous (scaberulous at the tips under high power), acute, often slightly awned (awns to 0.2 mm. long), hyaline, faintly 1-nerved; lemmas 2.5–2.6 (usually about 2.5) mm. long, 3-nerved, pubescent on the lower two-thirds of the midvein and lower margins (rarely with hairs between the nerves below), bearing an awn from below the tip, 0.7–1.7 (this usually more than 1) cm. long, flexuous; callus of lemma sparsely pilose; palea a little shorter than the lemma, sparsely pubescent on the lower two-thirds between the keels.

Holotype in the U.S. National Herbarium, no. 995888, collected on clay hill, Guatemala City, Guatemala, alt. 1,500 m., December 2, 1911, by A. S. Hitchcock (no. 9063).

Distribution: Rocky hillsides and exposed pine-oak areas, at elevations of 2,000–4,500 ft. Apparently common in Guatemala and Honduras.

GUATEMALA: Huehuetenango: W. of Aguacatán, on the road to Huehuetenango, *Standley* 81190 (F). Alta Verapaz: Sequanquím, *Cook & Doyle*

60 (US). ZACAPA: Volcán Gemelos, *Steyermark* 43251 (F). CHIQUIMULA: Between Chiquimula and Montaña Barriol, 3–15 miles NW. of Chiquimula, *Steyermark* 30649 (F, US). JALAPA: Vicinity of Jalapa, *Standley* 76731 (F, US). GUATEMALA: Guatemala City, *Hitchcock* 9063 (US holotype); *Hitchcock* 9064 (US); *Hitchcock* 9109. JUTIAPA: Between Jutiapa and Plan de Urrutia, *Standley* 75582 (F).

HONDURAS: COMAYAGUA: Between Comayagua and Villa San Antonio, *Archer* 3842 (CAS). FRANCISCO MORAZÁN: 30 km. W. of Tegucigalpa, *Archer* 3846 (US). Río Yeguare at about longitude 87° W. and latitude 14° N., *Molina* 1593 (US). Río Yeguare a Danlí, *Rodríguez* 1564 (F, GH). Above El Zamorano, *Standley* 14630 (F); *Standley* 24850 (F). San Antonio del Oriente, above San Antonio, *Swallen* 10968 (US). Mt. Uyuca, beyond Las Floras, *Swallen* 11323 (US). EL PARAÍSO: Mt. Yuscarán, *Molina* 605 (F, GH, US). Güinope, *Rodríguez* 1848 (F). Las Casitas, road to Güinope, *Swallen* 11081 (US). Road to Danlí, beyond Río San Francisco, *Swallen* 11216 (US). Road to Yuscarán, *Swallen* 11359 (US); *Swallen* 11367 (US). 5 km. S. of Ojo de Agua, *Williams & Molina* 11220 (F, GH, US). CHOLUTECA: San Marcos, *Williams & Molina* 10921 (F, GH, MICH, MO, US).

Muhlenbergia breviligula is distinguished by the very short ligule, long-awned lemmas pubescent on the lower two-thirds of the midnerve and margins, and spikelets usually 2.5 mm. or longer. In overall aspect it resembles most closely *M. emersleyi*, but in that species the ligule is usually 1 cm. or longer, the blades are considerably broader at the base, and the basal sheaths are not so persistent and fibrillose when old. *Muhlenbergia aurea* is closely allied by the very short ligule and long-awned lemmas; however, its spikelets are small, 2–2.2 mm., and the lemmas are only pubescent toward the base.

20. Muhlenbergia aurea Swallen. Contr. U.S. Nat. Herb. 29:411. 1950.

Strongly caespitose perennial; culms stout, glabrous, becoming scaberulous to scabrous toward the panicle, about ¾ m. tall, glabrous beneath the nodes; basal sheaths compressed-keeled, glabrous at the base, becoming scabrous toward the collar; ligule a short membranous rim appressed against the blade and hardly noticeable, 0.3–1.5 mm. long; sheath auricles rudimentary, 0.8–3 mm. long; blades of the culm to 42 cm. long, flat or folded, 2.5–5 mm. wide when unfolded, the upper surface scaberulous, the lower surface scabrous, the edges of the blade saw-toothed; upper throat scabrous; collar scabrous.

Panicle nodding, dense, golden yellow, about 36 cm. long, 7–9 cm. wide, the floriferous branches of the panicle appressed; axis scabrous; primary branches of the panicle 15–17 cm. long, secondary branches 4–6 cm. long, tertiary branches 1.5–2 cm. long; pedicels 1.5–2 mm. long, scabrous; spikelets 1.7–2.2 (mostly 2–2.2) mm. long; glumes about equaling the lemma, the second a little longer than the first, scabrous, very acute or slightly awn-tipped, especially the second glume, hyaline, 1-nerved; lemmas 1.9 mm. long, pubescent on the

lower third of the midvein and margins, acute, indistinctly 3-nerved, bearing an awn from just below the tip, mostly 1–1.5 cm. long; callus of the lemma with short hairs; palea a little shorter than the lemma, glabrous.

Holotype in the Field Museum of Natural History, no. 1057948, collected on lower south-facing slopes of Volcán Santa María de Jesús and Calahuache in thickets at base of vertical slopes along r. r., Dept. of Quezaltenango, Guatemala, alt. 1,300–1,500 m., Dec. 31, 1939, by J. A. Steyermark (no. 33175). A fragment of the holotype and photo are in the U.S. National Herbarium.

DISTRIBUTION: Known only from the type collection.

Muhlenbergia aurea is distinguished by the very short ligule, slightly awn-tipped glumes that equal the floret, and long-awned lemmas pubescent on the lower third of the midnerve and margins. In the original description the author remarked, "*Muhlenbergia aurea* is probably most closely related to *M. scoparia* Vasey, which differs in having much narrower sheaths and blades, an elongate ligule, a narrow, less densely flowered, purple panicle, and longer awns." Although related to *M. scoparia*, its closest relative appears to be *M. breviligula*, with which it shares the characteristics of a very short ligule and subequal slightly awn-tipped glumes (in *M. breviligula* the glumes are acute or occasionally somewhat awn-tipped). In *M. scoparia* the ligule is usually 1 cm. long or more and the glumes are unequal, a little shorter than the floret, and longer awn-tipped. *Muhlenbergia aurea* and *M. breviligula* occur much farther south than *M. scoparia*. *Muhlenbergia aurea* is known only from the type collection in Guatemala, *M. breviligula* from Guatemala and Honduras, and *M. scoparia* from northern and central Mexico.

21. Muhlenbergia grandis Vasey. Contr. U.S. Nat. Herb. 1:283. 1893.

Epicampes grandis (Vasey) Beal. Grasses N. Amer. 2:309. 1896. Based on *Muhlenbergia grandis* Vasey.

Epicampes bourgaei var. *grandis* (Vasey) Jones. Contr. West. Bot. 14:7. 1912. Based on *Muhlenbergia grandis* Vasey.

Caespitose perennial; culms glabrous, 88–164 (mostly 100–150) cm. tall; nodes 4, pubescent below (rarely above); basal sheaths compressed-keeled, glabrous, the old ones inflated, papery, brown or usually reddish brown, becoming fibrillose; ligule membranous, lacerate, 1.5–6 mm. long; sheath auricles lacking; blades of the culm 15–34 (mostly about 30) cm. long, flat or folded, 3–8 mm. wide when flat (usually 3–5 mm.), the upper surface of the blade scaberulous to scabrous, the lower surface scaberulous to scabrous, the upper and lower surfaces of the same blade alike; upper throat pubescent; collar a fringe of short white appressed hairs, rarely glabrous.

Panicle erect or somewhat nodding, usually very dense, the panicle branches mostly appressed, the groups of branches borne at intervals along the axis, yellowish or yellowish brown, 30–63 (usually 30–50) cm. long, 2–8 (usually 4–5) cm. wide; axis scaberulous, sometimes with a few hairs, ribbed, the primary branches to 9 (usually 7–9) cm. long, the secondary branches 1.5–4.5 cm. long, the tertiary branches 1–2 cm. long; pedicels of the lateral spikelets 0.5–1.5 mm. long, those of the terminal spikelets longer, to 2.5 cm., glabrous to scabrous, at least scaberulous under the spikelet; spikelets 1.3–2.5 (usually 1.5–2) mm. long; glumes usually about equal to the floret, equal or subequal (the second a little longer than the first), glabrous to scaberulous, roundish at the tips, somewhat erose at the tips (under high power), awnless, hyaline, nerveless; lemmas 1.5–2.2 (usually 1.8–2.1) mm. long, glabrous except for hairs on the lower part of the midnerve, acutish at the tip, 3-nerved, bearing a flexuous awn from below the tip, 6–19 (usually more than 10) mm. long; callus of lemma conspicuously short-pilose; palea a little shorter than the lemma, glabrous or with a few hairs at the base between the keels.

Type in the U.S. National Herbarium, no. 73222, collected in Río Blanco, Jalisco, Mexico, 1886, by Edward Palmer (no. 515).

DISTRIBUTION: Rocky mountainsides and rocky slopes of barrancas and canyons, at elevations of 3,000–5,000 ft. Of limited distribution in western Mexico, occurring from Sonora, south into Nayarit and Jalisco.

MEXICO: *Palmer* 170, in 1885 (TAES), in 1885 (GH, NY). SONORA: Cañon Estrella, Dist. Alamos, *Gentry* 332 M (MICH). NAYARIT: 10 mi. SE. of Tepic, *McVaugh* 13377 (MEXU, SMU, US). 10 mi. SE. of Ahuacatlán, *McVaugh & Koelz* 743 (MICH). JALISCO: SW. Autlán, *Hernández* 4637 (CHAP, US). 1–2 mi. N. of Ahuacapán, *McVaugh* 19531 (MICH, US). Ca. 8 mi. S. of La Resolana, *McVaugh* 21086 (MICH, US). Río Blanco, *Palmer* 415, in 1886 (F), 515, in 1886 (US type), 515a, in 1886 (GH, MO, US), 682, in 1886 (GH, NY, US). Guadalajara, *Pringle* 1760 (F, UC, US, paratypes), 2362 (ARIZ, CAS, GH, MICH, SMU, UC, US), 2765 (F, MO, UC, US fragment), 11751 (CAS, F, GH, MICH, MO, US). 2 mi. W. of Tequila, *Reeder & Reeder* 4205 (US, YU).

Muhlenbergia grandis is distinguished by the reddish-brown basal sheaths, collar a dense fringe of short hairs, the short spikelets, and long-awned lemmas short-pilose on the callus. It appears to be most closely related to *M. scoparia* with the reddish-brown sheaths unique to both species; the short spikelet, long-awned lemma, and short-pilose callus are features of both. The glumes of *M. grandis* are about equal and shorter than the floret, but are unequal in *M. scoparia*, long-awned, and about equal to the floret. The ligule of *M. grandis* is usually no more than 6 mm., as opposed to 8–16 mm. long in *M. scoparia*.

22. Muhlenbergia distans Swallen. N. Amer. Fl. 17(6):461. 1935

Muhlenbergia pubescens (H. B. K.) Hitchc. N. Amer. Fl. 17(6):460. 1935 (as to description only, not as to name).

Caespitose perennial; culms erect, 66–154 cm. tall, glabrous below, becoming scaberulous or scabrous below the panicle; nodes 2–4 on the lower part of the culm, puberulent to pubescent below, especially of the lower nodes; basal sheaths compressed-keeled, glabrous, the keels scaberulous; ligule membranous, firmer below but not decurrent, lacerate above, 0.5–1.5 cm. (usually 5–10 mm.) long; sheath auricles lacking; blades of the culm 11–62 (usually 25–40) cm. long, folded, narrow, 1–5 (mostly 2–3) cm. wide when flat, the edges saw-toothed; upper surface of blade mostly scaberulous, the lower surface mostly scabrous; upper throat scaberulous to scabrous; collar scaberulous to scabrous (mostly scaberulous).

Panicle erect, narrow, greenish brown, 24–40 cm. long, 1.5–4 (usually 2–4) cm. wide, the densely flowered branches ascending, floriferous almost to the base; axis scabrous; primary branches 5.5–9 cm. long, the secondary branches 1–5 (mostly 2–3) cm. long, the tertiary branches mostly 0.5 cm. long; pedicels scabrous, especially just below the spikelet, shorter than the spikelet, those of the lateral spikelets about 1 mm. long, those of the terminal spikelets 1.5–2 mm. long; spikelets 2.7–3.6 (usually 3–3.3) mm. long; glumes broadly acute at the tip, rarely a bit dentate, glabous-appearing with a roughened surface, the second glume 1–4 mm. longer than the first, indistinctly 1-nerved; lemmas acutish, 2.7–3.4 mm. long, shorter than the glumes, lightly pubescent on and between the nerves over the lower part, the upper part scabrous, the lateral margins densely pubescent toward the base, 3-nerved, the median nerve in many or all of the florets of the panicle extending from below the tip into a short awn, 1.5–5 (at least less than 5) mm. long; palea pubescent on the lower part.

Holotype in the U.S. National Herbarium, no. 746297, collected on dry hills, Las Sedas, Oaxaca, Mexico, alt. 6,000 ft., Sept. 15, 1894, by C. G. Pringle (no. 5575). Isotype at F.

DISTRIBUTION: Rocky slopes and barrancas, in the pine-oak zone, at elevations of 5,000–8,500 ft. Ranging in Mexico from Durango and San Luis Potosí southeastward into Guatemala. Apparently infrequent.

MEXICO: DURANGO: (?) Navíos, *Reeder, Reeder, & Soderstrom* 3379 (US, YU). (?) Llano Grande, *Reeder, Reeder, & Soderstrom* 3396 (US, YU), 3397 (US, YU), 3398 (US, YU). ZACATECAS: W. of Zacatecas on highway to Villanueva, *Soderstrom* 724 (US). SAN LUIS POTOSÍ: 8 mi. W. of Santa Catarina, *Reeder & Reeder* 4103 (US, YU). SW. of San Luis Potosí on road to Aguascalientes, *Reeder, Reeder, & Goodding* 1387 (YU). SW. of San Luis Potosí, *Reeder, Reeder, & Soderstrom* 3327 (US, YU), 3331 (US, YU). Puerta Huerta in the Sierra de

Alvarez, *Sohns* 1044 (US). JALISCO: Paso de Troje, SW. of Ojuelos on road to Aguascalientes, *McVaugh* 16801 (MICH, US). HIDALGO: Pachuca, *Hitchcock* 6708 (US); *Purpus*, Sept. 1905 (UC). Ixmiquilpan, *Purpus* 1466 (UC). *Puebla:* Cerro Tepoxuchil, *Arsène* 1901 (GH, MO, US). Acatzinco, Distrito de Tepeaca, *Arsène* (*Bro. Amable*) 2265 (MO, US). Fort de la Guadalupe, *Arsène* (*Bro. Nicolas*) 5436 (US). Between haciendas Santa Barbara and Cristo, *Arsène*, Aug. 1, 1907 (MO, US). Esperanza, *Hitchcock* 6485 (US). NE. of Zacatecas, *Soderstrom* 486 (US). TLAXCALA: Km. 70 de la carretera Apizaco-México, *Guerrero*, Sept. 25, 1962 (IPN). MEXICO: "Pédregal près Mexico," *Bourgeau* 683(?), 1865–1866 (US fragment ex P). Tenancingo, *Matuda* 28985 (US). DISTRITO FEDERAL: Xochitepec, *García* 86 (IPN). Lomas de Santa Fe, *Lyonnet* 55 (GH, MO, NY, US). Barrancas de Mixcoac, *Lyonnet* 2369 (US). Zacatepec, pedregal de Tlalpan, *Matuda* 21358 (US). Near Tlalpan, *Rose, Painter, & Rose* 8255 (US). On pedregal, *Rose, Painter, & Rose* 9456 (US). Tacubaya, *St. Pierre* 313 (MICH, US). Tacubaya, Dolores, *St. Pierre* 862 (MICH, US), 866 (MICH, US), 869 (US). Jajalpa, *St. Pierre*, 929 (CAS, MICH, US). MICHOACÁN: N. of Loma del Zapote, *Arsène*, Sept. 26, 1909 (MO, US). OAXACA: De Las Sedas a Felix Mahuaca, *Conzatti* 4870 (CAS). Las Sedas, *Pringle* 5574 (F), 5575 (US holotype, F isotype); *Smith* 916 (MO).

GUATEMALA: ZACAPA: Sierra de las Minas, below Finca Alejandria, *Steyermark* 29773 (F).

Muhlenbergia distans is distinguished by the greenish-brown spikelets, usually 3 mm. long or more, lemmas pubescent on the lower part, on and between the nerves, and ligules mostly 5–10 mm. long. The panicles are narrow, densely flowered, and have a distinctive brownish color. The basal sheaths are characteristically dark brown and firm when old. Apparently it is most closely related to *M. versicolor*, having in common the relatively greenish spikelets consisting of subequal glumes, lemmas pubescent on and between the nerves, and nodes pubescent below. In *M. versicolor* the glumes are often awn-tipped (especially the longer second glume) but only slightly dentate at the tip and not awned in *M. distans*. The lemmas of *M. versicolor* bear long awns on all the spikelets of the panicle; in typical *M. distans* short-awned and awnless spikelets occur in the same panicle. Moreover, *M. versicolor* is generally characterized by sheath auricles, which are lacking in *M. distans*.

Muhlenbergia distans was described from a specimen collected on dry hills, Las Sedas, Oaxaca, Mexico, in 1894 and has been known only from the type collection. It is a small tufted perennial with narrow culms and panicles with loosely ascending branches. The brownish spikelets range in length from 2.7–3.5 mm., the somewhat scaberulous glumes are acutish, and the short-awned lemmas are lightly villous on and between the nerves for a greater part of the length, with densely pubescent margins. Specimens previously referred to *M. pubescens* (H.B.K.) Hitchc. appear to belong to this species. As the name *M. pubescens* (H.B.K.) Hitchc. is untenable for these specimens, *M. distans* Swallen is the proper epithet. The majority of

cited specimens differ from the type of *M. distans* in being more robust and having thicker culms and denser panicles. However, the basic characters are similar, for the brownish spikelets are about 3 mm. long, the short-awned lemmas are pubescent on and between the nerves, although the pubescence is confined mostly to the lower half, and the ligules are about 5–10 mm. long. The holotype of *M. distans* appears to represent a smaller than typical and less robust representative of the species. *Conzatti* 4870, collected near the type locality, is more robust and has larger panicles than the type and is in all respects more like the majority of specimens referred to *M. distans*. Such differences as size and looseness versus denseness of panicles are variable characters within species of *Epicampes*. The spikelet and ligule are the more stable characters and are of greater importance in referring these specimens to *M. distans*.

Three collections (*Reeder, Reeder, & Soderstrom* 3379, 3396, and 3398) are doubtfully referred to *M. distans*. These specimens have long spikelets with the lemmas pubescent over the lower part and ligules about 1 cm. long. The habit of the panicles and plants, however, is more like that of *M. emersleyi* than of *M. distans*.

23. Muhlenbergia longiglumis Vasey. Contr. U.S. Nat. Herb. 1:283. 1893.

Caespitose perennial; culms glabrous, ¾–1 m. tall; nodes 2 (or 3?), pubescent below; basal sheaths compressed-keeled, glabrous, the old ones becoming brown and fibrous; ligule membranous, brownish and firmer on the lower part, thinner and lacerate above, 4–10 mm. or longer; sheath auricles lacking; blades of the culm 20–30 cm. long, folded, 1.5–2 mm. wide when flat; upper surface of the blade scaberulous to scabrous, the lower surface mostly scabrous (rarely glabrous); upper throat scabrous; collar scabrous.

Panicle erect or somewhat nodding, narrow, 20–40 (mostly about 30) cm. long, 1–2.5 cm. wide (excluding awns), the branches of the panicle about 3–3.5 cm. long, ascending, borne in verticils of approximate clusters of 2–6 at intervals along the axis, the body of the panicle light green, sharply contrasting with the dark purple awns; axis scaberulous, ribbed; pedicels of the lateral spikelets 2–3 mm. long, those of the terminal longer, scabrous on the narrow lower portion, pubescent on the swollen upper portion subtending the spikelet; spikelets 5–7 (mostly 6–7) mm. long; glumes about equal, a little longer than the floret, the surface with sparse short hairs, attenuate, awn-tipped (the awn 1 mm. long or less), grayish green, hyaline, 1-nerved; lemmas 4–5 mm. long, the margins densely pubescent on the lower ½–⅔, internerves glabrous or slightly pubescent near the base, remainder of lemma glabrous to scaberulous, lanceolate, 3-nerved, bearing a flexuous awn from below the tip, 2–6.5 cm. long;

callus of lemma bearing a dense ring of white hairs up to 1.5 mm. long; palea about equaling the lemma, glabrous or sparsely pubescent between the keels; anthers 3, yellow or greenish yellow, 2–3 mm. long.

Holotype in the U.S. National Herbarium, no. 2383429, collected near Guadalajara, Jalisco, Mexico, July–October 1886, by Edward Palmer (no. 766).

DISTRIBUTION: Rocky mountainsides in the pine-oak zone, at elevations of 5,000–7,000 ft. Apparently of limited distribution, all collections except one being from Jalisco; the one from Aguascalientes is from near the Jalisco border, and possibly on the Jalisco side.

MEXICO: *Palmer*, in 1886 (MO, may be part of *Palmer* 766 in 1886). AGUASCALIENTES: Sierra del Laurel, ca. 10 mi. SE. of Calvillo, *McVaugh & Koelz* 171 (MICH). JALISCO: 4–4.5 mi. NW. of Cuautla, road to Los Volcanes, *McVaugh* 20462 (MICH). Guadalajara, *Palmer* 766, in 1886 (US, holotype); *Pringle* 2365 (US), 11752 (GH, US).

Muhlenbergia longiglumis is distinguished by its awn-tipped, long glumes, light grayish green in contrast to the long dark purple awns of the lemmas, and lemmas glabrous except at the base. The purplish green panicle is not unlike that found in *M. versicolor*, although the species is probably most closely related to *M. emersleyi* with its long ligule, pyramidal panicle, and generally similar habit.

24. Muhlenbergia emersleyi Vasey. Contr. U.S. Nat. Herb. 3:66. 1892.

Muhlenbergia distichophylla sensu Vasey *in* Rothrock, Bot. Wheeler Surv. 283. 1878. Not *Podosaemum distichophyllum* J. S. Presl *in* K. B. Presl, Rel. Haenk. 1:231. 1830=*Muhlenbergia distichophylla* (J. S. Presl) Kunth. Description based on *Rothrock* 282 and 283.

Muhlenbergia vaseyana Scribn. Rep. Missouri Bot. Gard. 10:52. 1899. Based on *Muhlenbergia distichophylla* sensu Vasey, not *Podosaemum distichopyllum* J. S. Presl, 1830. Syntypes (by inference) *Rothrock* 282 and 283, from Rocky Canyon, Arizona, the basis of Vasey's description as cited above. *Rothrock* 282 is chosen as lectotype.

Epicampes stricta var. *distichophylla* sensu Jones, Contr. West. Bot. 14:6. 1912, in part as to the synonyms cited, *M. vaseyana* and *M. emersleyi*, not as to the basionym, *Podosaemum distichophyllum* J. S. Presl.

Epicampes emersleyi (Vasey) Hitchc. Bull. U.S. Dept. Agr. 772:144. 1920. Based on *Muhlenbergia emersleyi* Vasey.

Epicampes subpatens Hitchc. Bull. U.S. Dept. Agr. 772:144. 1920. (*Hitchcock* 13541, Guadelupe Mountains near Queen, New Mexico.)

Caespitose perennial; culms erect, narrow to thick, glabrous (rarely roughened), 1–1.5 meters, occasionally to 2 meters tall; nodes 3–4, glabrous or somewhat puberulent beneath; basal sheaths compressed-keeled, glabrous; ligule long, membranous, usually a little firmer at the base than above where thin and usually lacerated into narrow strands, ligules of the innovations long, narrow, and membranous throughout, conspicuous; sheath auricles lacking; blades of the culm 23–47 (mostly

20–40) cm. long, 2–6 mm. wide, flat or folded, the upper surface glabrous to scaberulous, the lower surface scabrous, at least the lower surface more scabrous than the upper surface of the same blade, the edges saw-toothed; upper throat scaberulous to scabrous (mostly scabrous); collar scaberulous.

Panicle typically lax above, the branches loosely ascending or spreading, the panicle pyramidal, light purplish to purplish tan, 20–40 (mostly 30–40) cm. long, 4–7 cm. wide (often much wider in the field); axis glabrous to scaberulous (rarely scabrous), the branches of all the orders naked below, the primary branches 9–17 (usually 9–12) cm. long, the secondary branches 3–9 (mostly 3–5) cm. long, the tertiary branches 0.5–4.5 (mostly 0.5–1.5) cm. long, quaternary branches sometimes present, as much as 2 cm. long; pedicels glabrous to scaberulous (sometimes scabrous), more scabrous just below the spikelet, pedicels of the lateral spikelets 0.5–1.5 mm. long, those of the terminal spikelets 1.5–3 mm. long; spikelets 2.2–3.2 mm. long, occasionally shorter or longer (usually 2.5–3, but most frequently 2.5–2.7 mm. long); glumes broadly acute, about equal to each other or the second glume 1–2 mm. longer than the first, mostly scaberulous to evenly scabrous, indistinctly 1-nerved; lemmas acutish, a little shorter than the glumes, pubescent on the midnerve and margins about one-half to three-quarters of the length, the pubescence varying from sparse to rather dense, that of the margins generally denser than that of the midnerve, the lemma 3-nerved, the middle nerve often excurrent from below the tip into an awn as long as 15 mm., generally purplish and flexuous, the awn persistent or deciduous, breaking off easily at the point of attachment to the lemma; palea a little shorter than the lemma, more or less pubescent between the keels for one-half to three-quarters of the length.

Type in the U.S. National Herbarium, no. 73223, collected in southern Arizona in 1890, "a coarse range grass that stock do not like," by J. D. Emersley (no. 46).

DISTRIBUTION: Rocky mountain slopes, barrancas, canyons, arroyos, and rocky ledges, at elevations of 4,500–7,500 ft., occurring most frequently at about 6,000–7,000 ft. The most common species of *Epicampes*, ranging from Texas to Arizona into northern Mexico, becoming less frequent south of Durango to Oaxaca.

UNITED STATES: TEXAS: Hueco, *Mulford* 80 (ILL, MO, NY). *Nealley*, in 1889 (DS, MICH, NY, UC, US), in 1890 (NY, US). "Common all over mts.," *Swallen* 1101 (US). Pine Spring, *Whitehouse* 8533 (US). "Expedition from western Texas to El Paso," *Wright* 729 (UC, US), 730 (GH, UC, US), 736 (US). BREWSTER COUNTY: Chisos Mountains, *Bailey* 392 (US). Green Gulch, *Berkman* Sept. 10, 1925 (TEX). Highway 223, *Brown* 30 (TEX). 6 mi. S. of Alpine, *Brown* 47 (TEX). N. of Alpine, *Carter* 19 (US). Blue Creek Trail, *Cory* 7272 (POM). Davis Mountains, 6 mi. W. of Alpine, *Cory* 40248 (TEX), 40413 (TAES).

Chisos Mountains, *Havard*, August 1833 (US). Alpine, *Hitchcock* 13594 (US). 5 mi. SW. of Marathon, *Johnston* 3336 (CAS, TEX). Elephant Mesa, *Johnston* 6427 (LL). Green Gulch, *Lundell* 13250 (LL, UC). Chisos Mountains, *Marsh* 56 (F). Lower Pine Canyon, *Marsh* 282 (GH, TAES, TEX), 322 (GH, TAES, TEX, US). Upper Pine Canyon, *Marsh* 351 (GH, TEX). Big Bend National Park, *Marsh* 51–1153 (TEX). Boot Spring, *Moore & Steyermark* 3181 (GH, MICH, MO, NY, UC, US). Emory Peak, *Mueller* 7850 (GH, MICH, NY, SMU, TAES, TEX, UC, US). Chisos Mountains, *Muller*, July 25, 1932 (DS, GH, UC). Blue Creek Canyon, *Parks & Cory* 7270 (TAES). Upper Blue Creek, *Parks & Cory* 7271 (TAES). Boot Ravine, *Parks & Cory* 30350 (TAES). Iron Mountain, *Parks & Cory* 30567 (TAES). Big Bend, *Reed* 90 (SMU), 99 (ARIZ). Iron Mountain, *Reed* 109 (UC), 112 (CAS). Hidden Valley, *Rose-Innes & Moon* 1266 (TEX). Big Bend National Park, *Shinners* 8799 (SMU). SR Hill, *Sperry* T487 (ARIZ, TAES). Green Gulch, *Sperry* 1805 (TAES). Casa Grande, *Warnock* 806 (DS, SMU). Mt. Emory, *Warnock* 12378 (TAES). McIntire Hill, *Warnock* 20270 (TEX). Split Tanks, *Warnock* 20766 (TEX). Baldy Peak, *Warnock* 20805 (TEX). Goat Mountain, *Warnock* 21470 (TEX). Old Marfa highway 2 mi. S. of Alpine, *Warnock* 21731 (TEX). S. of Alpine, *Warnock*, May 5, 1938 (ARIZ, GH). Blue Creek Canyon, *Wolff* 4693 (TAES), 4698 (F, TAES). Nail Place, *Young*, Aug. 7, 1915 (TEX). CULBERSON COUNTY: Guadalupe Mountains, *Bailey* 739 (US); *Havard*, in 1881 (US); *Silveus* 7674 (CAS, DS, SMU, TAES, TEX); *Young*, Sept. 5, 1916 (TEX). NE. of Pine Springs, *Correll & Johnston* 24231 (LL). McKittrick Canyon, *Moore & Steyermark* 3636 (CAS, DS, GH, MICH, MO, NY, UC, US); *Warnock* 10930 (ILL, LL, SMU), 12089 (LL, SMU). Mountains toward the Rio Grande, *Wright* 729 (GH). EL PASO COUNTY: Hueco Tanks, *Parks & Cory* 30973 (TAES); *Whitehouse*, Nov. 11, 1931 (TEX). Franklin Mountains, *Warnock* 14271 (LL, TEX). El Paso, *Whitehouse* 8531 (TEX). GILLESPIE COUNTY: *Reed*, January 1890 (MICH). HARDIN COUNTY: Camp Mountain, *Parks & Cory* 7093 (TAES). HUDSPETH COUNTY: Eagle Mountain, *Waterfall* 6341 (MO). JEFF DAVIS COUNTY: Davis Mountains, *Brown* 4213 (TEX); *Young* 20a (TEX), 40 (MO, US), Aug. 6, 1914 (TEX), Aug. 10, 1914 (GH, TEX). Fort Davis, *Carter* 61 (US); *Silveus* 7675 (CAS, SMU, TAES, TEX). Sawtooth Mountain, *Correll* 15008 (LL). Halloran, Nov. 29, 1940 (TAES). Mt. Livermore, *Hinckley* 101(MICH), July 1936 (ARIZ, GH, NY), Aug. 27,1939 (TEX). Limpia Canyon, *Nealley* 133 (DS, GH, ILL, MO, NY, POM, UC, US), in 1890 (US); *Reeder & Reeder* 4234 (YU); *Silveus* 294 (TAES, TEX). Castle Mountain, *Reeves* 1646 (TAES). Alpine-Ft. Davis, *Silveus* 824 (US). 15 mi. N. of Alpine, *Silveus* 825 (TAES, TEX). Mosquiz Canyon-Alpine-Ft. Davis road, *Silveus* 826 (CAS, TEX, US). McDonald Observatory, *Turner* 2970 (SMU). Scenic Loop of Davis Mountains, *Warnock* 9285 (LL, SMU). Mosquiz Canyon, *Warnock* 46557 (TEX). PRESIDIO COUNTY: Chinati Peak, *Correll & Johnston* 24378 (LL). 26 mi. SE. of Marfa, *Cory* 2852 (GH). Knox Canyon, *Hinckley* 2039 (SMU), July 20, 1941 (TEX). NEVADA: *Wheeler*, in 1872 (US). CLARK COUNTY: Las Vegas, *Arsène*, October 1925 (NY). NEW MEXICO: Gray, *Goodding* M–251.1 (US). *Vasey* (NY). *Wright* 1990 (CAS, GH, MO, NY, TAES, US). BERNALILLO COUNTY: Sandia Mountains, *Rominger* 16 (UNM). CATRON COUNTY: Mangas Canyon, *Metcalfe*, Sept. 15, 1896 (US), November 1896 (US). Tuloros Creek, *Olson* 439 (UC). Mogollon Mountains, *Rusby* 463 (ILL, MICH, MO, NY, UC, US), 597 (US). DONA ANA COUNTY: Dripping Springs, *Archer* 498 (MICH), *Dunn* 7284 (UNM). Organ Mountains, *Hitchcock* 3769 (US), 3795 (MICH, US); *Vasey*, August 1881 (US); *Wooton* 461 (DS, MO, NY, US), May 1891 (UNM), Sept. 17, 1893 (DS, UC, US), August 1894 (UNM), Sept. 17, 1903 (DS); *Wooton & Standley*, Sept. 23, 1906 (US). Mesilla Valley, *Fosberg* S–3674 (A, POM). Las

Cruces, *Griffiths* 7427 (US). Peña Blanca, *Standley*, Oct. 21, 1906 (US), Oct. 28, 1906 (US). Van Pattens Camp, *Wooton*, Sept. 10, 1899 (ILL). GRANT COUNTY: Mule Creek road, *Anderson & Rhinehart* 503 (TAES). Fort Bayard Watershed, *Blumer*, Nov. 18, 1905 (GH, NY, US). Black Range, *Goodding & Goodding* 381 (ARIZ). Silver City, *Greene* 439 (F, US), 440 (US). *Rusby*, in 1880 (US). Greenwood Cañon, *Smith*, Sept. 24, 1896 (US). "Copper-mines," *Wright* 1994 (GH, MO, NY, UC). HIDALGO COUNTY: Clanton Canyon, *Castetter* 10235 (UNM), 10244 (UNM). Little Hatchet Mountains, *Castetter* 10387 (UNM). Skeleton Canyon, *Castetter* 11256 (UNM). Coronado Forest S. of Animas, *Goodding* CG–14 (US). 20 mi. N. of Rodeo, *Goodding* M–248 (ARIZ, US). Below Animas Peak, *Goodding & Goodding* A–9775 (ARIZ, SMU), M–385 (ARIZ, LL). White Water, *Mearns* 352 (US). Dog Mountains, *Mearns* 2373 (US). Animas Valley, *Mearns* 2507 (US). LINCOLN COUNTY: S. of Fort Stanton, *Goodding & Goodding* M–183 (MO). OTERO COUNTY: Guadalupe ridge, *Chapline* 690 (US). Guadalupe Mountains, *Goodding & Goodding* M–201 (ARIZ, NY); *Hitchcock* 13541 (US holotype of *E. subpatens*). Gray's Ranch, *Goodding & Hardies* M–135 (MICH), M–136 (US), M–137 (ARIZ). Queen, *Hitchcock* 13500 (US), 13579 (US); *Amer. Gr. Nat. Herb.* 1382 (CAS, GH, LL, MO, UC), 1383 (CAS, GH, LL, MO, UC, US). SAN MIGUEL COUNTY: Las Vegas, *Anect* 198 (GH, NY, US); *Arsène* 17968 (UC); *Drouet & Richards* 3224 (F). SIERRA COUNTY: Lake Valley, *Beals*, in 1914 (MICH, US). Black Range, *Metcalfe* 1366 (CAS, F, GH, MO, NY, UC, US). SOCORRO COUNTY: Socorro, *Plank* 53 (US). 12 mi. S. of Magdalena, *Potter* 12 (UNM). ARIZONA: 3 mi. W. of Palominas, *Goodding*, Oct. 6, 1935 (ARIZ). Celero Mountains, *Griffiths* 6122 (MO, US). Stein's Pass, *Jones* 4219 (ARIZ, CAS, F, POM, UC, US). Wood's Ranch, *McDougal* 490 (US). Niggerhead Mountains, *Mearns* 1871 (US). *Miera* 1 (UNM). Devils Canyon, *Peebles, Harrison, & Kearney* 3200 (ARIZ). *Pringle*, June 17, 1884 (NY). Montezuma Wells, *Purpus* 8289 (MO, UC, US). "Explorations and surveys W. of the 100th. meridian," *Rothrock* 282 (GH syntype of *M. vaseyana*). "In all canyons," *Rusby* G(MO, NY). White Mountains, *Schroeder*, summer 1938 (ARIZ). *Vasey*, in 1889 (US). COCHISE COUNTY: Chiricahua Mountains, *Blumer* 68 (ARIZ). Paradise, *Blumer* 1698 (ARIZ, DS, F, GH, MO, NY, US). Upper Hunt Canyon, *Clark* 8457 (ARIZ). Upper Rhyolite Canyon, *Clark* 8510 (ARIZ). 8 mi. W. of Wilcox, *Darrow*, Sept. 10, 1942 (ARIZ, UC). Carr Canyon, *Darrow, Gould, Phillips, & Pultz* 1402 (DS), 2436 (ARIZ, CAS, UC, US). Black Canyon, *Goodding* 429–49 (ARIZ). Coyote Canyon, *Goodding* 1123–49 (ARIZ). Golden Eagle Box Canyon, *Goodding* 88–54 (ARIZ, UC), 30–55 (ARIZ). Huachuca Canyon, *Goodding* 709–58 (ARIZ). Huachuca Mountains, *Goodding* 251–62 (ARIZ); *Jones*, Sept. 3, 1903 (DS, POM). Guadalupe Canyon, *Gould & Haskell* 4540 (ARIZ, GH). Dragoon Mountains, *Griffiths* 1876 (ARIZ, US). Pearce, *Griffiths* 1957 (ARIZ, US). Ramsey Canyon, *Jones* 24736 (CAS, GH, MO, POM, UC), Sept. 30, 1929 (NY). Dos Cabezas, *McDougal* 778 (US). Pedregosa Mountains, *Mearns* 838 (US). San Simon, *Thornber* 2225 (ARIZ). Pine Canyon, *Toumey* 14 (US, YU), Sept. 10, 1896 (NY, US). Blue Canyon, *Toumey* 15a (US). Fort Huachuca, *Wilcox* 410 (US), 446 (TAES), in 1894 (NY, US). COCONINO COUNTY: Kaibab Forest, *Pase* 343 (US). GILA COUNTY: on road from Globe to Coolidge Dam, *Eastward* 16646 (CAS). Pocket Creek Canyon, *Gould* 3741 (ARIZ, GH, NY, UC, US). Parker Creek Canyon, *Gould & Hudson* 3867 (ARIZ). Pinal Mountains, *Shreve* 7454a (ARIZ). Pine, *Toumey* 67 (US), July 23, 1892 (ARIZ, DS, UC). GRAHAM COUNTY: 7 mi. S. of Stockton Pass road, *Anderson & Rhinehart* 603 (ARIZ). Clifton road, *Anderson & Rhinehart* 622 (ARIZ, TAES). Porter Springs, *Kessler* 485 (ARIZ, TAES). Graham Mountains, *Moeller* 186 (ARIZ, TAES). San Simon Valley, *Thornber*, Aug. 22, 1905 (ARIZ). MOHAVE COUNTY:

Hualpi Mountains, *Nichol*, Sept. 14, 1937 (ARIZ). PIMA COUNTY: Redingon Pass, *Benson* 9216 (ARIZ, DS, POM). Sabino Canyon, *Benson* 10559 (POM). Happy Valley Trail, *Blumer* 3453 (F). Sabino Trail, *Carter*, Nov. 20, 1932 (ARIZ). Soldier Canyon, *Darrow*, Sept. 27, 1936 (GH). Fresnal Canyon, *Gilman* 11 (ARIZ). Baboquivari Canyon, *Gilman* 17 (DS, NY, US). Prison Road, *Ginter*, Oct. 6, 1941 (UC). Coyote Mountains, *Goodding & Lusher* 97–45 (ARIZ, NY). About 25 mi. E. of Tucson, *Gould* 2565 (ARIZ, MO, UC, US). Santa Rita Forest Reserve, *Griffiths* 3437 (US), 5936 (ILL, US). Santa Catalina Mountains, *Griffiths* 7043 (US), 7047 (US), 7048 (US), 7149 (ILL, US), 7164 (US); *Pringle*, May 14, 1883 (MO, YU); *Thornber* 9217 (ARIZ). Baboquivari Mountains, *Jones* 24737 (CAS, GH, MO, POM, TEX, UC), Sept. 19, 1929 (NY). Molina Basin, *Leader & Leader* 228 (ARIZ). Redding Pass Road, *Leader & Leader* 371 (ARIZ). Baboquivari Canyon, *Peebles* 532 (ARIZ). Mt. Lemmon, *Peebles & Harrison* 2293 (MO). Rincon Mountains, *Pringle*, July 19, 1884 (CAS, F, GH, LL, NY, US). Soldier Canyon, *Shreve* 5420 (ARIZ, GH). White House Canyon, *Stewart*, Sept. 23, 1942 (NY). Soldiers' Trail, *Stewart*, Oct. 10, 1942 (NY). Floritas Canyon, *Streik* S–32 (ARIZ). Rosemont, *Thornber*, Sept. 30, 1901 (ARIZ, DS, UC). Tucson, *Toumey*, in 1892 (NY, UC, US). Reddington Pass, *Young*, Oct. 2, 1939 (ILL). PINAL COUNTY: Oracle, *Thornber*, Sept. 9, 19(?) (ARIZ). SANTA CRUZ COUNTY: Santa Rita Mountains, *Arnold & Arnold*, Aug. 23, 1939 (UC); *Griffiths* 7257 (US); *Griffiths & Thornber* 46 (US); *Jones*, Aug. 24, 1903 (POM, UC); *Thornber & Griffiths* 46 (ARIZ). Box Canyon, *Arnold*, Sept. 16, 1936 (GH). White House (Madera) Canyon, *Benson* 9732 (POM); *Graham* 3635 (DS); *Parker* 7079 (ARIZ). Stone Cabin Canyon, *Culley* 36 (ARIZ); *Thornber* 188 (ARIZ, DS, MO, NY, POM, UC), 5245 (ARIZ), Sept. 14, 1903 (UC). Sycamore Canyon, *Goodding* M–258 (LL, SMU); *Goodding & Goodding* 431 (ARIZ); *Parker* 7381 (ARIZ, ILL). Nogales, *Harris*, Sept. 19, 1927 (MO, POM); *Peebles & Harrison* 4695 (ARIZ). Patagonia, *Hitchcock* 3689 (US), 3719 (US), 3720 (US); *Kearney & Peebles* 10050 (MICH, US). Coronado National Forest, *Killip* 40854 (US). YAVAPAI COUNTY: Granite Dells, *Benham* M–95 (ARIZ); *Darrow*, Sept. 3, 1939 (ARIZ, UC). Mingus Mountain, *Benham* M–109 (MICH, YU); *Goodding* 174–46 (ARIZ, NY). Fort Whipple, *Coues & Palmer* 424 (MO). 10 mi. S. of Prescott, *Featherly*, July 18, 1929 (SMU). Prescott, *Kearney & Peebles* 9735 (ARIZ, US); *Purchase* 527 (MICH); *Thornber* 8644 (ARIZ); *Williams* 3037 (US).

MEXICO: *Palmer*, in 1886 (ARIZ). *Wilkinson* 9601 (F, NY, US). BAJA CALIFORNIA: El Taste, *Brandegee*, Sept. 13, 1893 (NY, UC, US), Nov. 1902 (UC). Sierra de San Francisquito, *Brandegee*, Sept. 24, 1899 (US), Sept. 29, 1899 (UC). Sierra de la Laguna, *Brandegee*, Oct. 4, 1899 (UC,US). Cerro de la Giganta, *Carter, Alexander, & Kellogg* 2025 (DS, GH, LL, MO, UC, US). Sierra de la Laguna, E. of Todos Santos, *Carter, Alexander, & Kellogg* 2382 (DS, GH, UC, US). SONORA: Cañon Estrella, *Gentry* 394 M (DS, MICH), Oct. 1, 1933 (US). Cerro del Capulin, NW. of Aribabi, *Harvey* 1688 (CAS, GH, MICH, MO, US). Estación de Tajo, *Hernández & Tapia* N–1569 (CHAP). San José Mountains, *Mearns* 962 (US). Sierra de los Alamos, *Palmer* 409, in 1890 (CAS, GH, US). Colonia Morelos, *Santos* 30 (US) 174 (US). 20 mi. W. of La Angostura, *Santos* 1798 (GH). El Tigre to El Rancho de Robles, *Santos* 1925 (ARIZ, GH, MICH, MO, NY, SMU, TEX, US). El Rancho de Robles to Colonia Morelos, *Santos* 1974 (ARIZ). El Puerto del Cumarito, *Santos* 2090 (GH, SMU, TEX). El Cañon de la Bellota, *Santos* 2109 (DS, SMU, TEX). El Picacho del Pilar, *Santos* 2166 (GH, SMU, TEX). Cañon del Agua Amarga, *White* 3631 (MICH). 8 mi. S. of Nogales, Sonora, *Wiggins* 7535 (DS, MICH, US). CHIHUAHUA: Arroyo Mesteño, Sierra del Nido, *Christman* 170 (UC). 15 mi. S. of Encinillas, *Correll* 23294 (LL). Minas Nuevas, *Correll & Gentry*

22736 (LL). Between Guadalupe y Calvo and Tecolote, *Correll & Gentry* 23237 (LL). Guasaremos, *Gentry* 1874 (ARIZ, F, GH, MEXU, MO, UC). Rancho Carretas, *Harvey* 1627 (CAS, GH, MICH, MO, US), 1641 (MICH). Km. 1773 carretera Cd. Juárez, *Hernández & Mathus* N–1837 (GH). Sánchez, *Hitchcock* 7669 (US), 7669 ½ (NY, US), 7714 (ILL, US). Miñaca, *Hitchcock* 7742 (US). Pirámide, *Johnston* 8118 (GH). Guayanopa Canyon, *Jones*, Sept. 24, 1903 (NY, POM). Río Gavilán, *Leopold* 225 (US). Majalca, *Le Sueur* Mex–021 (GH, MO, SMU, TEX, US). Chuhuichupa, *Le Sueur* Mex–087 (TEX). NW. of Chihuahua, *Le Sueur* 0149 (CAS, GH, MO, SMU, UC, US). 20 mi. SW. of Chuhuichupa, *Muller* 3594 (GH, LL, MICH, UC). Sierra Gazachic, SW. of Miñaca, *Pennell* 18957 (US). 15 mi. S. of Madera, *Reeder & Reeder* 2640 (YU). 23 mi. SE. of Chuhuichupa, *Reeder & Reeder* 2670 (YU), 2671 (YU). 37 mi. S. of Villa Matamoros, *Reeder, Reeder, & Soderstrom* 3449 (US, YU). 4 mi. E. of Parral, *Reeder, Reeder, & Soderstrom* 3457 (US, YU). 1 mi. E. of Cuauhtémoc, *Reeder, Reeder, & Soderstrom* 3467 (US, YU). 16 mi. W. of Cuauhtémoc, *Reeder, Reeder, & Soderstrom* 3469 (US, YU), 3470 (US, YU), 3471 (US, YU), 3472 (US, YU). 12 mi. N. of Chihuahua, *Reeder, Reeder, & Soderstrom* 3482 (US, YU), 3485 (US, YU). 15 mi. W. of Flores Magon, *Reeder, Reeder, & Soderstrom* 3499 (US, YU). 12 mi. W. of Colonia Juárez, *Reeder, Reeder, & Soderstrom* 3502 (US, YU), 3503 (US, YU). S. of Hernández, *Reeder, Reeder, & Soderstrom* 3524 (US, YU), 3533 (US, YU) NE. of Cuesta Blanca, *Reeder, Reeder, & Soderstrom* 3542 (US, YU), 3543 (US, YU), 3548 (US, YU), 3549 (US, YU). Parral, *Soderstrom* 828 (US, YU). San Francisco de Oro, *Soderstrom* 870 (US, YU), 871 (US, YU). 13 mi. SW. of Cuauhtémoc, *Soderstrom* 917 (US, YU), 918 (US, YU). 12 mi. N. of Chihuahua, *Soderstrom* 930 (US, YU). Sierra Hechiceros near the Coahuilan border, *Stewart* 202 (GH). Organos, *Stewart & Johnston* 2066 (GH). Casas Grandes, *Townsend & Barber* 357 (CAS, F, GH, ILL, MO, NY, POM, UC, US). Santa Eulalia Hills, *Wilkinson*, Aug. 25, 1885 (F, US), Sept. 21, 1885 (UC). COAHUILA: Corte Blanco fork of Charretera Canyon, *Johnston* 8950 (GH, MO). 2 mi. NE. of Nava, *Johnston & Graham* 4166 (TEX). La Noria, *Johnston & Muller* 462 (GH, LL), 587 (GH, LL). Del Carmen Mountains, *Marsh* 624 (GH, TEX, US), 655 (GH, TEX, US). Santa Rosa Mountains, *Marsh* 1511 (F, GH, TEX). Sierra de la Gloria, *Marsh* 1948 (F, GH, TEX). 1 mi. S. of Cuesta Blanca, *Reeder & Reeder* 3227 (YU). 26 mi. E. of Saltillo, *Reeder, Reeder, & Soderstrom* 3289 (US, YU). Jaral, *Schumann* 1753 (US). La Noria, *Stewart* 1208 (GH). Sierra del Carmen, Villa Acuña, *Wynd & Mueller* 594 (US). NUEVO LEON: Dulces Nombres, *Meyer & Rogers* 3092 (MO, US). Monterrey, *Mueller & Mueller* 385 (GH). Ca. 10 mi. E. of Galeana, *Reeder & Reeder* 3973 (US, YU). Mt. Mirador, *Roybal* 60 (US). 8 mi. N. of Escondido, *Shreve & Tinkham* 9714a (ARIZ). TAMAULIPAS: (?)El Rosario, *Bartlett* 10882 (CAS, GH, MICH, NY, POM). 11 mi. W. of Victoria toward Jaumave, *Johnston & Graham* 4141 K (TEX). (?)Sierra de Tamaulipas, at Santa María de los Nogales, *Martínez & Borja* F–1939, aff. *M. emersleyi* (TEX), F–2083, aff. *M. emersleyi* (TEX). SINALOA: Cerro Babuyo, *Gentry* 11420 (US). Ortega 3118 (US). 18 mi. E. of Santa Lucía, *Reeder & Reeder* 2469 (YU). DURANGO: 40 mi. S. of Durango, *Hernández, Ruppert, & Guevara* X–2558 (US). Durango, *Hitchcock* 7621 (US); *Palmer* 542, in 1896 (CAS, F, GH, MO, UC, US). Otinapa, *Palmer* 344, in 1906 (F, GH, NY, US), 553, in 1906 (US). 25 mi. W. of Durango, *Reeder, Reeder, & Soderstrom* 3440 (US, YU), 3441 (US, YU). 27 mi. SE. of Durango, *Soderstrom* 756 (US), 758 (US). SW. of Durango on Durango–Mazatlán road, *Soderstrom* 767 (US), 772 (US), 775 (US). 6 mi. N. of Durango, *Soderstrom* 787 (US), 789 (US). ZACATECAS: 6 mi. SW. of Carboneras, *Gentry* 8522. 15 mi. W. of Zacatecas, *Soderstrom* 725 (US). 25 mi. NW. of Fresnillo, *Soderstrom* 728

(US), 729 (US). Sombrerete, *Soderstrom* 734 (US), 735 (US), 746 (US), 753 (US). San Luis Potosí: 8 mi. W. of Santa Catarina, *Reeder & Reeder* 4104. SW. of San Luis Potosí, *Reeder, Reeder, & Soderstrom* 3303 (US, YU), 3324 (US, YU), 3325 (US, YU), 3326 (US, YU), 3330 (US, YU). Sierra de San Miguelito, *Sohns* 1140 (US), 1151 (US), 1157 (US), 1320 (US), 1465 (US). Sierra de Alvarez, *Sohns* 1385 (US). Aguascalientes: Rincón de Romos, *Reeder, Reeder, & Soderstrom* 3335 (US). Jalisco: Bolaños, *Rose* 3003 (US). 15 mi. SE. of Encarnación de Díaz, *Soderstrom* 694 (US), 697 (US). Guanajuato: Ojo de Agua, *Sohns* 252 (MICH, US). 6 km. E. of Guanajuato, *Sohns* 315 (MICH, US). Hidalgo: 18 mi. NE. of Zimapán, *Reeder & Reeder* 4121 (US, YU). Puebla: Cerro de Soluche, *Purpus* 4081 (F, GH, MO, NY, UC, US). Morelos: Km. 53 Autopista México–Cuernavaca, *Espinosa* 66 (IPN). Mexico: Naranjo, Temascaltepec, *Hinton* 1987 (NY, UC). Distrito Federal: Mixcoac, *St. Pierre* 905 (MICH, US). Michoacán: La Huerta, *Arsène*, Oct. 30, 1909 (NY). San Miguel, *Arsène*, Dec. 4, 1910 (NY). Oaxaca: Huahuapan de León, *Soderstrom* 413 (US), 414 (US), 447 (US).

Muhlenbergia emersleyi is distinguished by the typically long membranous ligule, lemmas pubescent on the midnerve and margins, palea pubescent between the keels, and the purplish, flexuous, more or less pyramid-shaped panicle. It appears to be most closely related to *M. lehmanniana* with their similar overall habit, long ligules, and lemmas pubescent on the lateral margins. *Muhlenbergia lehmanniana* differs in that the midnerve of the lemma is usually glabrous or if pubescent the hairs are sparse and rather inconspicuous; the palea is glabrous between the keels, rarely a few hairs are present. The panicles of *M. lehmanniana* are golden yellow but usually purplish in *M. emersleyi*. The callus is blunt or truncate at the base in *M. emersleyi* but more or less acute in *M. lehmanniana*. *Muhlenbergia emersleyi* is most common in southwestern United States and northern Mexico and has not been collected south of the Isthmus of Tehuantepec. South of the Isthmus, in Chiapas through Central America, the specimens with yellowish panicles are referable to *M. lehmanniana*. Comparison may also be made with *M. breviligula*, its ligule only a short rim or almost lacking. However, long ligules are sometimes found on the leaves of the innovations in the same plants that have the typically short ligule on the culm leaves. This suggests, perhaps, the ancestral nature of a long ligule in this species and points to a close relationship with *M. emersleyi*.

The awned condition of the lemmas requires further study. Awned and awnless specimens, alike in all other respects, were collected side by side (e.g., *Pennell* 18957, *Greene* 439 and 440, awnless and awned forms; and *Nealley* 133, slightly awned and very long-awned specimens). In this species the condition of the awn is not correlated with other characters to separate the awned from the awnless plants. The length of the awn is also quite variable. The author has collected plants side by side; in one the awns were short (*Reeder, Reeder*, &

Soderstrom 3548) and in the other very long (*Reeder, Reeder, & Soderstrom* 3543). All of the specimens I have seen from Baja California and Sonora, Mexico, are long-awned.

An awnless form of this species from New Mexico (*Hitchcock* 13541) served as the type for *Epicampes subpatens* Hitchc. In the type specimen the spikelets are about 3 mm. long, the glumes whitish and scabrous, and the lemmas densely pubescent on the midnerve and margins. Although most of the spikelets are awnless, some bear a rudimentary awn from just below the tip. The branches of the panicle are stiffer than those of the type of *M. emersleyi* (*Emersley* 46) and the panicle is not lax. With this exception no basic difference exists between the two specimens. Hitchcock, who described *E. subpatens*, later placed it in synonymy with *M. emersleyi*.

Three specimens deserve special comment. *Bartlett* 10882 (Sierra de San Carlos, Tamaulipas, Mexico) has an inflorescence much like that of *M. emersleyi* with long-awned spikelets in which the lemmas have the typical pubescence pattern of the species. However, the basal sheaths in many specimens are not strongly compressed-keeled, the ligule is firm below and membranous above, and the blades are narrow and folded, reminiscent in these latter features of *M. gooddingii*. Although it looks distinctive, no basic characters separate this specimen from the *M. emersleyi* complex. Two additional specimens, *Martínez & Borja* F–1939 and F–2083 (Sierra de Tamaulipas), are quite distinctive, but I can find no good characters to separate them from the *M. emersleyi* complex. Further collections of *Epicampes* from the state of Tamaulipas may clarify the position of these unusual specimens. I have seen only four specimens from the whole state.

Muhlenbergia emersleyi is the most common species of *Epicampes* and the most variable. Attempts to segregate the forms into more than one species on the basis of morphology are unrewarding because of a thorough intergradation of characters among the specimens. An intensive cytological investigation of this species complex will be necessary before we can be certain of the precise nature and extent of the various races present.

25. Muhlenbergia xanthodas Soderstrom, **sp. nov.**

Perennis caespitosa, culmis robustis erectis glabris 60–90 cm. altis, nodis 3 glabris, vaginis inferioribus compressis et robuste carinatis basin versus glabris adversum collum scaberulis; ligula membranacea (ad basin firma), margine versus apicem lacerata, usque ad 30 mm. longa; laminis culmi angustis attenuatisque conduplicatis utrinque scabris, ca. 70 cm. longis; collis scabris; panicula erecta angusta aurea, 23–27 cm. longa, usque ad 3 cm. lata, ramis appressis ad basin florescentibus, axe glabro, ramis primariis usque ad 4.5 cm.

longis, secundariis usque ad 1.5 cm. longis, tertiariis usque ad 5 mm. longis, pedicellis glabris infra spiculam scaberulis quam spiculis brevioribus; spiculis 2–3 (plerumque 2–2.5) mm. longis, glumis acutissimis fere aequalibus, quam flosculo paullo longioribus, glabris lucidis paene translucentibus enerviis, lemmatibus acutis, 2–2.7 mm. longis, glabris nisi quod puberulentis lateribus ad basin, nervis 3, infra apicem aristas, 6–10 mm. longas, aureas ferentibus, callo brevipiloso.

A *M. lehmanniana* Henr. ramis paniculae brevioribus et magis appressis, et glumis glabris lucidis (paene translucentibus) sine nervis differt.

Caespitose perennial; culms stout, erect, glabrous, 60–90 cm. tall; nodes 3, glabrous beneath; basal sheaths strongly compressed-keeled, glabrous below, becoming scaberulous toward the collar; ligule membranous (somewhat firm at the base), lacerate above, as short as 0.5 mm. on the lower culm leaves, to as much as 30 mm. on the higher culm leaves; sheath auricles lacking; blades of the culm to 70 cm. long, narrow and long-attenuate, tightly folded, 1.5–2 mm. wide when unfolded, the upper and lower surfaces scabrous; upper throat scabrous; collar scaberulous.

Panicle erect, narrow, golden yellow, 23–27 cm. long, to 3 cm. wide, the branches of the panicle strongly appressed, floriferous almost to the base; axis glabrous; primary branches to 4.5 cm. long, the secondary branches to 1.5 cm. long, the tertiary branches to 5 mm. long; pedicels shorter than the spikelet, glabrous, scaberulous beneath the spikelet; spikelets 2–3 (mostly 2–2.5) mm. long; glumes acute, about equal to each other, a little longer than the floret, glabrous, shining, almost translucent, nerveless; lemmas acute, 2–2.7 mm. long, glabrous except for short hairs toward the base of the lateral margins, 3-nerved, the middle nerve extending into a golden awn from below the tip of the lemma, 6–10 mm. long; callus of lemma short-pilose; palea equal to or a little longer than the lemma, glabrous.

Holotype in the U.S. National Herbarium, no. 1817864, collected on rock on Mt. Ovando, Chiapas, Mexico, at 2,300 meters altitude, November 14–18, 1939, by Eizi Matuda (no. 4003). Isotypes at F, MICH.

DISTRIBUTION: Known only from Chiapas, Mexico, from the type and from the following additional collection:

MEXICO: CHIAPAS: Between Escuipulas and Cañada Honda, *Hernández & Sharp* X–311 (US).

Muhlenbergia xanthodas appears to be most closely related to *M. lehmanniana* which ranges from Costa Rica to Colombia. Both species are like *M. emersleyi* in general habit and both also have long-awned lemmas, pubescence on the margins of the lemma at the base,

and long membranous ligules. In *M. emersleyi* the lemma is pubescent on the midnerve and the margins, the panicles and awns of the lemma are generally purplish. In *M. xanthodas* and *M. lehmanniana* the lemma is short-pilose at the base, but the midnerve of the lemma is glabrous or bears relatively few inconspicuous hairs, and the panicles are golden, the rather straight awns of the lemmas are golden, and the strongly compressed-keeled sheaths are golden. In typical *M. emersleyi* the paleas are pubescent between the keels, but in *M. xanthodas* and *M. lehmanniana* the paleas are glabrous. *Muhlenbergia xanthodas* is distinct from *M. lehmanniana* in its much shorter, closely appressed panicle branches, producing a very dense panicle; in *M. lehmanniana* the branches are longer and spreading. The glumes of *M. xanthodas* are glabrous, shining (almost translucent), and nerveless; the glumes of *M. lehmanniana* are scabrous and 1-nerved.

The specific epithet is from the Greek words *ξανθός*, yellow or golden, and *δάς*, torch, in allusion to the dense golden panicles.

26. Muhlenbergia lehmanniana Henr. Med. Rijksherb. Leiden 40:59. 1921.

M. multinodis Asplund. Bot. Not. 1939: 796. f. 1. 1939.
M. attenuata Swallen. Ann. Missouri Bot. Gard. 30:138. 1943.

Caespitose perennial; culms glabrous to scaberulous, 72–167 cm. tall; nodes 3–4, glabrous beneath; basal sheaths compressed-keeled, glabrous, tightly imbricate, flat, golden yellow, not becoming brown and shredded; ligule somewhat firm at the base, becoming long and membranous, conspicuous from side view, slightly decurrent, 1 cm. long, to as long as 2.5 cm., enclosed in the folded blade above, entire below and for the greater part of its length; sheath auricles lacking or rarely rudimentary ones present, no more than 0.1 mm. long; blades of the culm folded, long and narrow, becoming threadlike toward the tip, 1.5–4 mm. wide when flat, the upper surface of the blade slightly scaberulous to scabrous, the lower surface scaberulous to scabrous; upper throat scabrous; collar scaberulous to scabrous.

Panicle erect, usually dense, the branches ascending 19–40 cm. long, 3–6 cm. wide, generally golden, golden brown, or purplish green; axis scaberulous to scabrous; the primary branches 3.5–12 (rarely to 19) cm. long, the secondary branches 1–5 (mostly 1–2) cm. long, tertiary branches usually lacking (rarely to 1.5 cm. long); pedicels of the lateral spikelets 0.7–2 mm. long, those of the terminal spikelets relatively long, 2–4 mm., scaberulous to scabrous, especially just beneath the spikelet; spikelets 2–3.5 (usually about 2.5) mm. long; glumes longer than the floret, the second glume usually a little longer than the first, mostly scabrous, blunt at the tip or slightly dentate (under high power), usually slightly awn-tipped, the awns to 0.3 mm., hyaline, 1-nerved (1 or 2 additional faint nerves sometimes

present); lemmas 1.8–3 (mostly about 2.5) mm. long, glabrous dorsally except at the base of the midvein, the lower part of the margins conspicuously short-pilose, acutish at tip, 3-nerved, the awns straight, or somewhat flexuous, over 1 (to 3.5) cm. long; callus of the lemma short-pilose; palea a little shorter than the lemma, glabrous or at most with a few hairs at the base between the keels.

Holotype in the Rijksherbarium, Leiden, collected near Popayán, Cauca, Colombia, by F. C. Lehmann, no. B. T. 1267 (in Herb. Lugd. Bat. under no. 908. 350–519). Fragments of type ex K in the U.S. National Herbarium, no. 72978, ex L, no. 72977, and ex. Herb. Lugd. Bat. (L), no. 72979. Isotype at NY.

DISTRIBUTION: Hillsides and barrancas at elevations of mostly between 2,500 and 6,000 ft. One label states "from 100 m.," another "10,000 ft.," but I doubt if the species is found at these extremes. Rather common from Costa Rica, south and eastward into Colombia.

COSTA RICA: *Tonduz* 4630 (US). Las Cóncavas, *Lankester* 676 (US) *Oersted* 14065 (F, US), 14171 (US). Bord du chemin de Mano de Tigre, *Pittier* 4630 (US). Buenos Aires, Canton de Osa, *Valerio* 873 (F). PUNTARENAS: Savanes de Cañas Gordas, *Pittier* 7355 (US), 7358 (US), 11019 (US). ALAJUELA: San Pedro de San Ramón (cerca del Río Barranca), *Brenes* 21415 (F, NY). SAN JOSÉ: Tablazo hasta 1800 m., *Valerio* 1052 (F). CARTAGO: Tejar, *Solis* 618 (44) (F). Mount Irazu, *Oersted* 14012 (US).

PANAMA: CHIRIQUÍ: El Boquete, *Hitchcock* 8174 (US holotype of *M. attenuata*). Grassy hillsides, *Hitchcock* 8241 (US). Foothills, *Hitchcock* 8242 (US). Barranca, road toward Dolega, *Hitchcock* 8340 (US). Cerro Vaca, *Pittier* 5360 (US), 5362 (US). COCLÉ: S. of El Valle de Antón, *Allen* 2812 (GH, MO, US). Vicinity of Olá, *Pittier* 5042 (US), *Pittier* 5062 (US).

COLOMBIA: ANTIOQUIA: Medellín, *Bro. Daniel* 246 (US). Barbosa, vicinity of Medellín, *Toro* 697 (US). VALLE: Cordillera Occidental, Hoya del Río Cali, *Cuatrecasas* 18737 (F, US). CAUCA: Popayán, *Lehmann* B.T. 1267 (US fragments of type ex K and L, NY isotype). Loma de Bichiquí near Toribió, *Pittier* 1468 (US). El Tambo, *von Sneidern* 1323 (S holotype of *M. multinodis*), A. 231 (A).

Muhlenbergia lehmanniana is distinguished by the long ligule, pyramidal panicles of spikelets with scabrous glumes, long-awned lemmas pubescent only at the base, paleas glabrous between the keels, and calluses acute rather than truncate.

This species looks much like *M. emersleyi* and has been confused with it. The panicles of long-awned spikelets resemble some forms of *M. emersleyi*. However, a number of characters differentiate the two species. *Muhlenbergia lehmanniana* occurs in the mountains of Costa Rica through Panama and into the Colombian Andes; *M. emersleyi* is most abundant in southwestern United States and northern Mexico, becoming less frequent southward into Mexico until, beyond the Isthmus of Tehuantepec, it disappears. The basal sheaths of *M. lehmanniana* are distinctly flabellate and golden,

more so than *M. emersleyi*, and the blades are long, narrow, and attenuate, rather threadlike at the ends. The acute callus of the floret distinguishes this species from *M. emersleyi*. The hairs on the callus and lower part of the margins of the lemma and midnerve (where confined) are longer individually than in *M. emersleyi*. In that species the hairs usually extend about two-thirds up the lemma. In most specimens of *M. lehmanniana* the palea is glabrous but pubescent on a half to two-thirds of its length in *M. emersleyi*.

Swallen's *M. attenuata*, although distinctive because of the unusually long panicle branches long-naked at the base, is evidently an extreme form of this species, and the type of *M. multinodis* unquestionably fits within the morphological range of *M. lehmanniana*.

Muhlenbergia lehmanniana is closely related to *M. xanthodas* which differs in the nerveless, glabrous, almost translucent glumes, and short, appressed panicle branches. The ranges of both species are well separated, *Muhlenbergia xanthodas* being known only from Chiapas.

Species Described as *Epicampes* but Excluded from Section *Epicampes*

Epicampes argentea (Vasey) Jones. Contr. West. Bot. 14:7. 1912.=**Muhlenbergia argentea** Vasey. Bull. Torrey Club. 13:232. 1886. A weak, somewhat decumbent perennial with rounded basal sheaths [SW. Chihuahua, Mexico].

Epicampes arundinacea (Trin. [error for Griseb.]) Hack. Anal. Mus. Nac. Buenos Aires 11:107. 1904.=**Sporobolus rigens** (Trin.) Desv. in C. Gay. Fl. Chile 6:295. 1853. [Chile.]

Epicampes buchingeri Fourn. Mex. Pl. 2:88. 1886.=An annual **Muhlenbergia** (from description; type not seen). [Mexico.]

Epicampes clomena (Trin. [error for Kunth]) Jones. Contr. West. Bot. 14:7. 1912.=**Muhlenbergia peruviana** (Beauv.) Steud. Nom. Bot. ed. 2. I:41. 1840. An annual [Peru].

Epicampes coerulea Griseb. Abh. Ges. Wiss. Göttingen 19:256. 1874=?**Muhlenbergia angustata** (Presl) Kunth. Rev. Gram. I. (Supp.): xvi. 1830. [Colombia to Argentina.]

Epicampes coerulea var. *submutica* Hack. ex Stuck. Ann. Mus. Nac. Buenos Aires 13:471. 1906.=?**Muhlenbergia angustata** (Presl) Kunth. 1830. Rev. Gram. I (Supp.): xvi. [Colombia to Argentina.]

Epicampes crassiculmis Piper. Proc. Biol. Soc. Wash. 18:144. 1905.=**Sporobolus wrightii** Munro ex Scribn. Bull. Torrey Club 9:103. 1882. [USA, Mexico.]

Epicampes kunthiana Griseb. Abh. Ges. Wiss. Göttingen 19:256. 1874.=**Muhlenbergia angustata** (Presl) Kunth. Rev. Gram. I (Supp.): xvi. 1830. [Colombia to Argentina.]

Epicampes macroura (H.B.K.) Benth. Journ. Linn. Soc. Bot. 87. 1881. =**Muhlenbergia macroura** (H.B.K.) Hitchc. A member of section *Podosemum*. [Mexico and Guatemala.]

Epicampes mexicana (Scribn.) Jones. Contr. West. Bot. 14:7. 1912. =**Muhlenbergia biloba** Hitchc. Contr. U.S. Nat. Herb. 17:294. 1913. An annual [Mexico].

Epicampes phleoides (H.B.K.) Griseb. Abh. Ges. Wiss. Göttingen 19:256. 1874.=**Muhlenbergia angustata** (Presl) Kunth. 1830. Rev. Gram. I (Supp.): xvi. [Colombia to Argentina.]

Epicampes rigens Benth. *in* Journ. Linn. Soc. Bot. 19:87. 1881.=**Muhlenbergia rigens** (Benth.) Hitchc. A member of section *Podosemum*. [SW. USA and Mexico.]

Epicampes rigens (Trin.) Phil. Anal. Mus. Nac. Chile sect. II(8):82. 1891. Based on *Vilfa rigens* Trin. which=**Sporobolus rigens** (Trin.) Desv. *in* C. Gay. Pl. Chile 6:295. 1853. [Chile.] Not *Epicampes rigens* Benth. Journ. Linn. Soc. 19:87. 1881. [USA, Mexico.]

New Species and New Combination

Muhlenbergia gooddingii Soderstrom, sp. nov.
Muhlenbergia inaequalis Soderstrom, sp. nov.
Muhlenbergia iridifolia Soderstrom, sp. nov.
Muhlenbergia reederorum Soderstrom, sp. nov.
Muhlenbergia virletii (Fourn.) Soderstrom, comb. nov.
Muhlenbergia xanthodas Soderstrom, sp. nov.

Voucher Specimens Examined

Specimens used in the study of leaf anatomy, embryos, and lodicules are listed below. The letters in the herbarium citation indicate the study for which the specimen was used (A=leaf anatomy: cross section and/or epidermis, E=embryo, and L=lodicule). The author was fortunate to have access to the John R. Reeder collection, indicated by (R), of slides and drawings of many grasses.

Muhlenbergia

M. andina (Nutt.) Hitchc. USA: Arizona: Grand Canyon Natl. Park, North Rim, along Point Sublime Road, *Reeder* 1808 (YU): L.

M. angustata (Presl) Kunth. ECUADOR: Cañar, near the village of San Marcos, *Camp* E–2519 (NY): A, L.

M. arenicola Buckl. MEXICO: Chihuahua: Plains near Chihuahua, *Pringle* 479 (NY): A, L.

M. argentea Vasey. MEXICO: Chihuahua, *Palmer* 160, in 1885 (US holotype): A.

M. arizonica Scribn. MEXICO: Durango: N. of Cd. Durango, *Reeder* 2602 (YU): A(R).

M. articulata Scribn. MEXICO: San Luis Potosí: Cárdenas, *Pringle* 3913 (NY): A, L.

M. asperifolia (Nees & Mey.) Parodi. USA: New Mexico: Albuquerque, *Hardies* M–103 (YU): A(R).

M. biloba Hitchc. MEXICO: Chihuahua: Near Chihuahua, *Pringle* 819 (NY): L.

M. breviligula Hitchc. GUATEMALA: Jalapa: Vicinity of Jalapa, *Standley* 76731 (F): A.

M. brevis C. O. Goodding. MEXICO: Chihuahua: 12 miles W. of Cuauhtémoc, *Reeder* 2620 (YU): L(R).

M. brevivaginata Swallen. MEXICO: JALISCO: 6 mi. NW. of Cuautla, *McVaugh* 13671 (US holotype): A.

M. capillaris (Lam.) Trin. USA: FLORIDA: Near Highland View, *Kral & Godfrey* 54211 (NY): L. TEXAS: Bastrop State Park, *Silveus* 2396 (YU): A(R).

M. confusa (Fourn) Swallen. MEXICO: CHIHUAHUA: 10 miles N. of Largo, *Reeder* 2684 (YU): A(R).

M. crispiseta Hitchc. MEXICO: DURANGO: 23 miles W. of Cd. Durango, *Reeder* 2545 (YU): A(R).

M. curvula Swallen. MEXICO: GUANAJUATO: 12 mi. from Guanajuato on road to Santa Rosa, *Moore* 1353 (US holotype): A.

M. depauperata Scribn. MEXICO: GUANAJUATO: 11 miles S. of San Miguel Allende, *Reeder* 2279 (YU): L(R).

M. distans Swallen. MEXICO: DISTRITO FEDERAL: Lomas, *Lyonnet* 55 (NY): A. OAXACA: Las Sedas, *Pringle* 5574 (NY): A, L.

M. distichophylla (Presl) Kunth. MEXICO: JALISCO: Near Guadalajara, *Pringle* 2346 (NY): A, L. GUERRERO: Vallecitos, Montes de Oca, *Hinton* 11635 (NY): A.

M. dubia Fourn. MEXICO: MEXICO: 12 miles E. of Ixtlahuaca, *Soderstrom* 509 (YU): A, L.

M. dubioides C. O. Goodding. MEXICO: CHIHUAHUA: 12 miles N. of Chihuahua, *Soderstrom* 931 (YU): A.

M. elongata Scribn. MEXICO: CHIHUAHUA: Near Chihuahua, *Pringle* 938 (NY): A.

M. emersleyi Vasey. MEXICO: ZACATECAS: 13 miles W. of Sombrerete, *Soderstrom* 746 (YU): A, L.

M. erectifolia Swallen. COLOMBIA: SANTANDER: Páramo de Santurbán, near Vetas, *Killip & Smith* 17470 (US holotype): A.

M. eriophylla Swallen. MEXICO: MEXICO: Luvianos, Temascaltepec, *Hinton* 5307 (US holotype): A.

M. expansa (DC.) Trin. USA: SOUTH CAROLINA: 5 miles S. of Georgetown, *Godfrey* 8151 (NY): A, L. NORTH CAROLINA: Wilmington, *Amer. Gr. Nat. Herb.* 1374 (NY): A, E.

M. filiculmis Vasey. USA: COLORADO: Green Mountain Falls, *Sheldon* 321 (US holotype): A.

M. firma Beal. MEXICO: HIDALGO: Pachuca, *Amer. Gr. Nat. Herb.* 1351 (NY): A, L.

M. flexuosa Hitchc. PERU: Huacachi, estación near Muna, *Macbride* 3874 (US holotype): A.

M. frondosa (Poir.) Fernald. USA: CONNECTICUT: New Haven (no voucher): L.

M. gigantea (Fourn.) Hitchc. MEXICO: DURANGO: 22 miles E. of Santa Lucía, *Reeder* 2488 (YU): A, L. JALISCO: Near Guadalajara, *Pringle* 3335 (NY): A, E; 8 miles W. of Guadalajara, *Soderstrom* 607 (YU): A.

M. glabrata (H. B. K.) Kunth. MEXICO: PUEBLA: San Marcos, *Amer. Gr. Nat. Herb.* 1356 (NY): A, L.

M. glomerata (Willd.) Trin. USA: CONNECTICUT: 6 miles W. of Tolland, *Reeder* 944 (YU): L.

M. grandis Vasey. MEXICO: JALISCO: Near Guadalajara, *Pringle* 2765 (NY): A, E, L.

M. hintonii Swallen. MEXICO: MEXICO: Crucero, Temascaltepec, *Hinton* 3059 (US holotype): A.

M. holwayorum Hitchc. BOLIVIA: Sorata, *Rusby* 201 (NY): A.

M. involuta Swallen. USA: TEXAS: Boerne-Bandera Road, N. of San Antonio, *Silveus* 780 (NY): A(R), L.

M. jaliscana Swallen. MEXICO: Jalisco: Sierra de Manantlán (15–20 mi. SE. of Autlán), *McVaugh* 13991 (US holotype): A.
M. lindheimeri Hitchc. USA: Texas: 15 miles S. of San Antonio, *Burr* 513 (NY): A, L.
M. longiglumis Vasey. MEXICO: Jalisco: *Pringle* 2365 (NY): A, L.
M. longiligula Hitchc. USA: Arizona: Chiricahua Mts., Barfoot Park, *Blumer* 1424 (NY): A. MEXICO: Chihuahua: 38 miles S. of Casas Grandes, *Reeder* 2699 (YU): A, E; 31 miles W. of Colonia Juárez, *Reeder* 3222 (YU): L.
M. lucida Swallen. MEXICO: Chihuahua: Sierra Gazachic 35 km. SW. of Miñaca, *Pennell* 18955 (US holotype): A.
M. macrotis (Piper) Hitchc. MEXICO: Jalisco: *Pringle* 2360 (NY): E. Guerrero: Petlacala, S. of Reyes, *Mexia* 9098 (NY): A, L.
M. macroura (H. B. K.) Hitchc. MEXICO: Michoacán: Quinceo, near Morelia, *Arsène*, Nov. 11, 1909 (F): E; 14 miles E. of Morelia, *Soderstrom* 551 (US): L. Chiapas: Chiquihuite, Vol. Tacana, *Matuda* 2829 (NY): A.
M. matudae Sohns. MEXICO: Morelos: Lago de Zempoala, *Matuda* 25601 (US holotype): A.
M. metcalfei Jones. USA: New Mexico: Grant County, Santa Rita Mountains, *Metcalfe* 1485; (US holotype): A.
M. mexicana forma *ambigua* (Torr.) Fernald. USA: Connecticut: New Haven (no voucher): L.
M. montana (Nutt.) Hitchc. MEXICO: Sonora: Trail from El Tigre to El Rancho de Robles, *Santos* 1924 (NY): A. Michoacán: Morelia, *Arsène* 5811 (NY): L.
M. aff. *montana* (Nutt.) Hitchc. MEXICO: Durango: 7 miles E. of El Salto, *Reeder* 2572 (YU): A(R).
M. nigra Hitchc. MEXICO: Distrito Federal: Serrania de Ajusco, *Pringle* 6676 (NY): A. Near Cima, *Pringle* 11739 (NY): L. GUATEMALA: Volcán de Agua, *Cook*, May 12, 1905 (NY): E.
M. orophila Swallen. GUATEMALA: Huehuetenango: Cerro Chemal, summit of Sierra de los Cuchumatanes, *Steyermark* 50309 (US, holotype): A.
M. palmeri Vasey. MEXICO: Chihuahua: Sierra Madre, *Pringle* 1417 (NY): A, L.
M. peruviana (Beauv.) Steud. PERU: Arequipa: July 11, 1946, *Pearson* 1: (YU): A(R).
M. plumbea Scribn. *in* Beal. MEXICO: Mexico: 17 miles E. of Toluca, *Reeder* 2218 (YU): A(R).
M. pubescens (H. B. K.) Hitchc. MEXICO: Jalisco: 15 miles SE. of Encarnación de Díaz, *Soderstrom* 692 (YU): A, 693 (YU): E. Tlaxcala: Sta. Ana Chiautempan, *Arsène*, 10–11–1908 (NY): E. Puebla: 5 miles NE. of Zacatepec, *Soderstrom* 483 (YU): L.
M. pulcherrima Scribn. *in* Beal. MEXICO: Durango: 15 miles E. of Ciudad, *Reeder* 2535 (YU): A(R).
M. purpusii Mez. MEXICO: San Luis Potosí: Near km. 549, 36 mi. S. of Matehuala, *McVaugh* 18204 (US): A.
M. quadridentata (H. B. K.) Kunth. MEXICO: Mexico: Temascaltepec, Las Cruces, *Hinton* 4389 (NY): A, L.
M. racemosa (Michx.) B. S. P. USA: En route from Fort Duchesne to Dakotah, *Cornman*, in 1888 (NY): L.
M. reverchonii Vasey & Scribn. USA: Texas: S. of Austin, *Silveus* 2478 (YU): A(R), L.
M. richardsonis (Trin.) Rydb. USA: Colorado: Leadville, *Goodding* M–3272 (YU): A(R).

M. rigens (Benth.) Hitchc. USA: Arizona: Chiricahua Mts., Riggs' Ranch, *Blumer* 1491 (NY): E. MEXICO: Chihuahua, 27 miles NW. of Madera, *Reeder* 2662 (YU): A. Zacatecas: 25 miles NW. of Fresnillo, *Soderstrom* 731 (YU): A, L.

M. rigida (H. B. K.) Kunth. MEXICO: Jalisco: 2 miles W. of Guadalajara, *Soderstrom* 640 (YU): L. Zacatecas: 2 miles W. of Sombrerete, *Soderstrom* 743 (YU): A, L.

M. robusta (Fourn.) Hitchc. MEXICO: Jalisco: Near Guadalajara, *Pringle* 2321 (NY): E. Michoacán: Punguato, near Morelia, *Arsène* (NY): L. Mexico: Temascaltepec, Carboneras, *Hinton* 1853 (NY): A. 3 miles NW. of Tlamanaco, *Soderstrom* 382 (YU): L. Chiapas: 20 miles E. of Chiapa de Corzo, *Reeder* 2128 (YU): A. GUATEMALA: Chimaltenango: Near Chimaltenango, *Standley* 59136 (F): E.

M. schreberi Gmel. USA: Connecticut: New Haven (no voucher): A(R), L.

M. scoparia Vasey. MEXICO: Sinaloa: Mesa Malqueson, Cerro Colorado, *Gentry* 5178 (NY): L; 10 miles E. of Santa Lucía, *Reeder* 2451 (YU): E.

M. setifolia Vasey. USA: Texas: Guadalupe Mountains, *Havard* 9 (US, holotype): A.

M. aff. *speciosa* Vasey. MEXICO: Durango: 21 miles E. of Santa Lucía, *Reeder* 2476 (YU): A, L.

M. stricta (Presl) Kunth. MEXICO: Jalisco: La Granja, near Guadalajara, *Soderstrom* 642 (YU): A, L.

M. subaristata Swallen. MEXICO: Durango: El Salto (Aserraderos), Sierra Madre Occidental, *Pennell* 18572 (US holotype): A.

M. sylvatica (Torr.) Torr. ex Gray. USA: Connecticut: New Haven (no voucher): L(R).

M. torreyana (Schult.) Hitchc. USA: New Jersey: Egg Harbor, *Bissell* (NY): A(R), L.

M. torreyi (Kunth) Hitchc. USA: New Mexico: Capitan, *Goodding* M–189 (YU): L.

M. uniflora (Muhl.) Fernald. USA: New York: Wading River, *Miller* 130 (NY): L. New Hampshire: Chatham, *Johnson*, August 7, 1927: A(R).

M. versicolor Swallen. MEXICO: Oaxaca: Sierra de San Felipe, *Smith* 927 (NY): L.

M. virletii (Fourn.) Soderstr. MEXICO: Mexico: Sultepec, *Hinton* 3219 (NY): A, L.

M. wrightii Vasey. USA: New Mexico: Soil Conservation Service Nursery, Albuquerque (seed from Flagstaff, Arizona), *Goodding and Hardies* A–6498 (YU): L.

M. xerophila C. O. Goodding. USA: Arizona: Forest Cabin Canyon, Baboquivari Mountains, *Goodding* A–9493 (YU): L; Moristo Canyon, Baboquivari Mts., *Goodding* 443–45 (NY): A.

Genera Other Than Muhlenbergia

Agrostis alba L. USA: Connecticut: Guilford, *Dudley*, July 17, 1904 (YU): L.

Agrostis scabra Willd. USA: Continental Divide, near Beardshead, *Goodding*, July 25, 1939 (YU): E(R).

Blepharoneuron tricholepis (Torr.) Nash. USA: Arizona: Tiyo Plateau, Grand Canyon, *Reeder* 1807 (YU): L(R).

Cinna arundinacea L. USA: Connecticut: New Haven (no voucher): L. New Jersey: Plainfield, *Tweedy*, September 1881 (YU): E(R).

Lycurus phleoides H. B. K. MEXICO: Jalisco: 11 miles N. of Ciudad Guzmán, *Reeder* 2352 (YU): L(R).

Polypogon monspeliensis (L.) Desf. USA: MASSACHUSETTS: Lowell, *Swan*, July 14, 1880 (YU): L. BELGIUM: Ripe fruits received from Hortus Botanicus Bruxellensis in 1955: E(R).

Sporobolus asper (Michx.) Kunth. USA: CONNECTICUT: East Haven, *Nichols*, Aug. 31, 1912 (YU): L(R).

Sporobolus heterolepis (A. Gray) A. Gray. USA: CONNECTICUT: West Rock, *Nichols*, Sept. 5, 1911 (YU): L(R).

Sporobolus wrightii Munro ex Scribn. USA: ARIZONA: San Pedro, *Toumey*, July 25, 1894 (YU): L; ripe fruits collected by *L. N. Goodding*, October 1955: E(R).

Stipa avenacea L. USA: MASSACHUSETTS: Boston, Blue Hills Reservation, *Reeder* 233 (YU): E(R), L(R).

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Podosemum, sect., 95, 102, 104, 111, **112**, 113, 117, 122, 177, 178
Podosemum, subg., **111**, 112, 113, 122
Polypogon, 81, 84, 97, 100, 101, 107, 108, 110
monspeliensis, 99, 105, 182
Sphaerocaryum, 84
Sporoboleae, 79, 80, 84
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Sporobolus, 78, 79, 81, 82, 83, 84, 93, 97, 100, 101, 107, 108, 109, 110, 111
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heterolepis, 105, 182
rigens, 177, 178
wrightii, 80, 99, 105, 177, 182
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Stipeae, 79, 80, 81, 109
Triplachne, 84
Urochondra, 84
Vilfa rigens, 178

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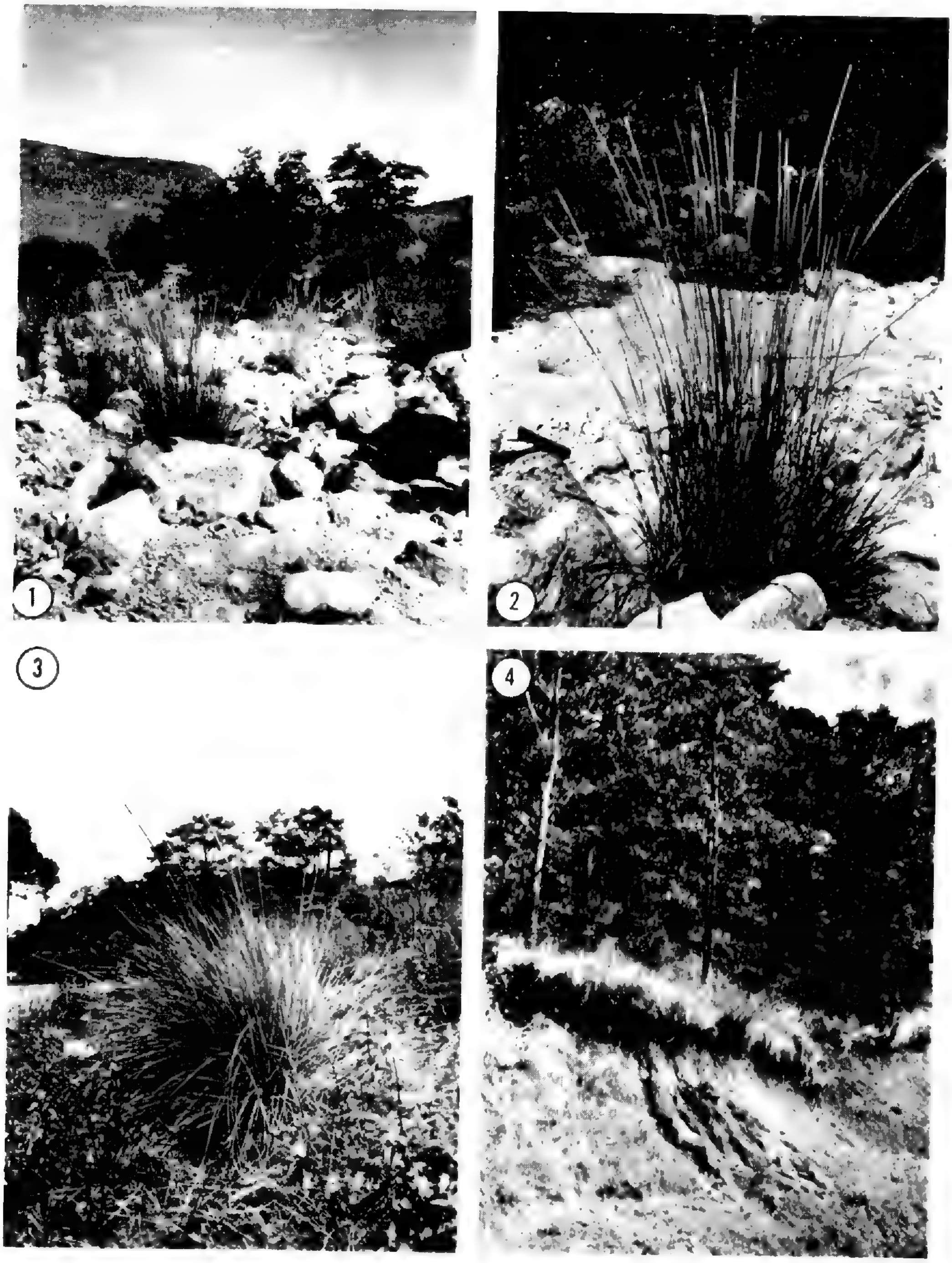
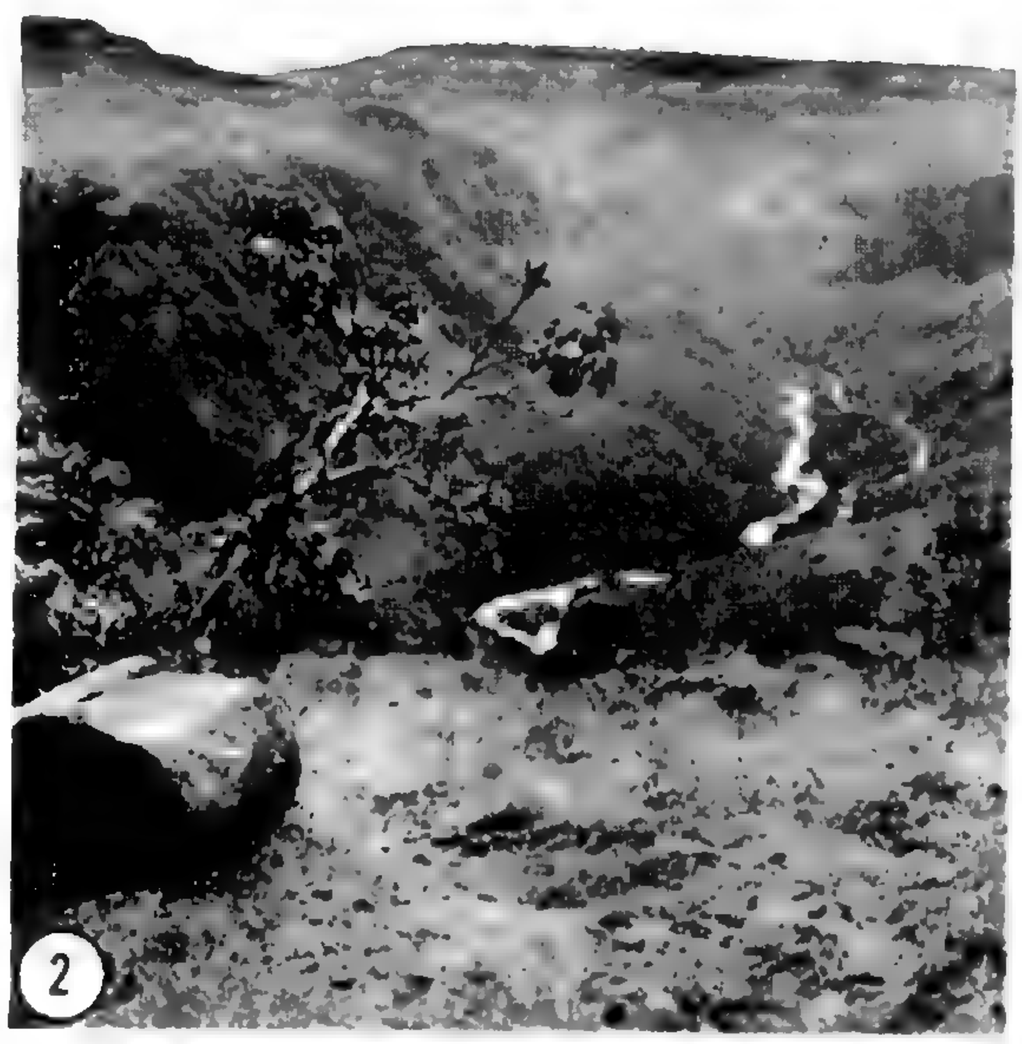
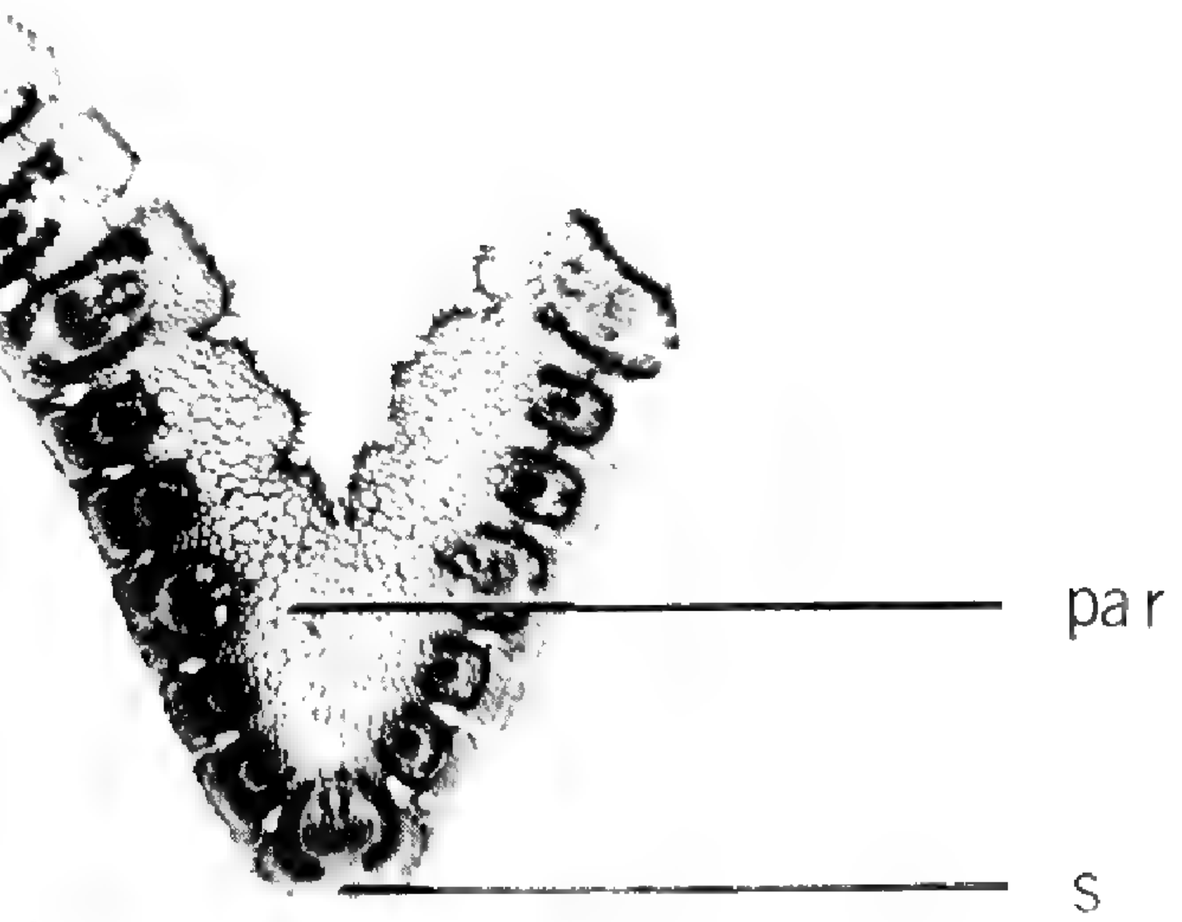


Muhlenbergias, *Podosemum* section: FIG. 1.—*Muhlenbergia rigens* among rocks in a dry streambed, 12 mi. W. of Chihuahua, Chihuahua, Mexico, alt. 4,800 ft. (*Soderstrom* 927–929). FIG. 2. *M. rigens*, closeup of *Soderstrom* 927. FIG. 3.—*M. macroura*, pine-zone area with volcanic soil, La Joya, Veracruz, Mexico, alt. 7,000 ft. (*Soderstrom* 478). FIG. 4.—*M. macroura* on eroded bank at edge of pine-oak hillside, 14 mi. E. of Morelia, Michoacán, Mexico, alt. 6,700 ft. (*Soderstrom* 551).

Muhlenbergias, *Epicampes* section: Fig. 1.—*Muhlenbergia emersleyi* (awnless) near ledge of arroyo, 15 mi. SE. of Encarnación de Díaz, Jalisco, Mexico, alt. 7,000 ft. (*Soderstrom* 697). Fig. 2. Clump of *M. emersleyi* (long awned) growing in protection of "maguey silvestre" (*Agave* sp.), plateau near San Francisco de Oro, Chihuahua, Mexico, alt. 7,060 ft. (*Soderstrom* 870). Fig. 3. *M. robusta*, upper ledge of arroyo, 6 mi. E. of Santa Cruz, Jalisco, Mexico, alt. 5,300 ft. (*Soderstrom* 566). Fig. 4.- *M. distans*, rocky ledge of arroyo, 15 mi. W. of Zacatecas, Zacatecas, Mexico, alt. 7,200 ft. (*Soderstrom* 724).



Habitats of Muhlenbergias, subgenus *Podosemum:* FIG. 1.—Clumps of *M. pubescens* are common on the rocky desert hillside near Durango, Durango, Mexico, alt. 6,200 ft. FIG. 2. Barranca de Oblatos near Guadalajara, Jalisco, Mexico. Many early C. G. Pringle collections of *Muhlenbergia* came from this and nearby barrancas; an area of Mexico that appears to be the center of distribution of the genus. FIG. 3.—*M. rigens* is found at the base and *M. emersleyi* higher on the ledges of a dry arroyo, 25 mi. NW. of Fresnillo, Zacatecas, Mexico, alt. 7,300 ft. FIG. 4.—Large clumps of *M. robusta* not yet in bloom, 3 mi. NW. of Tlamanalco, Mexico, Mexico, alt. 7,000 ft. (*Soderstrom* 380 collected here).



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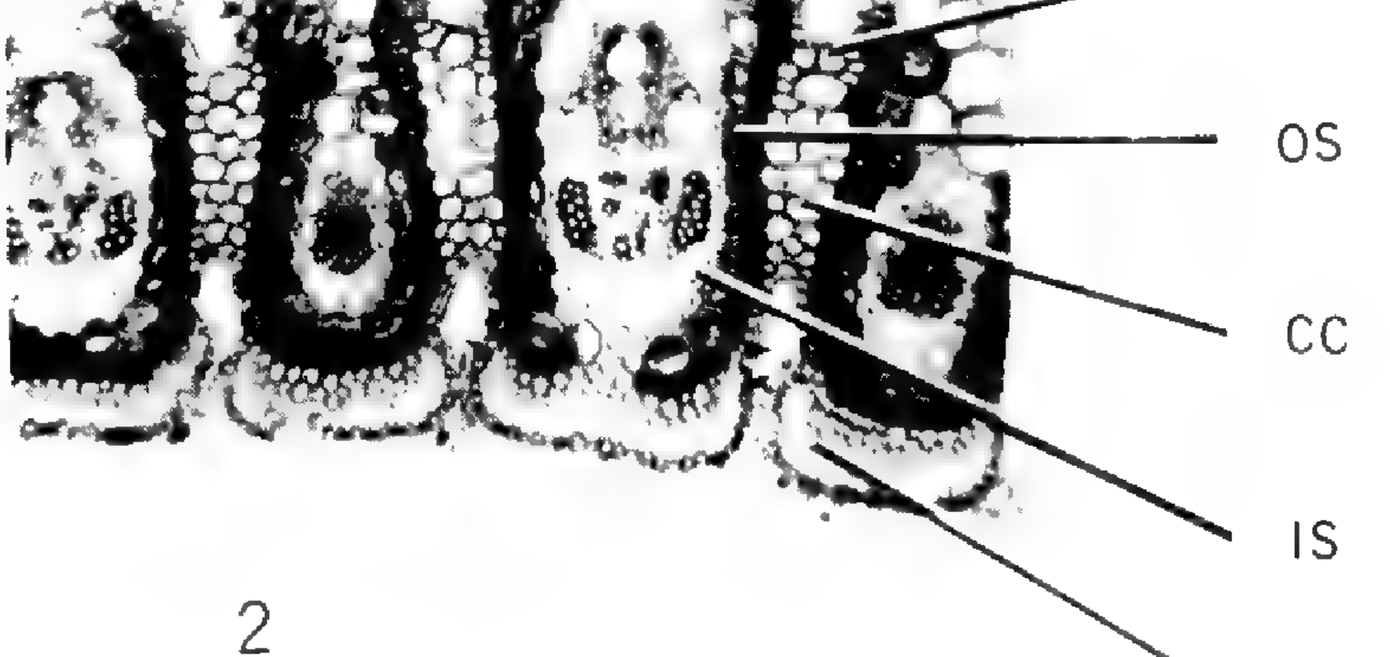

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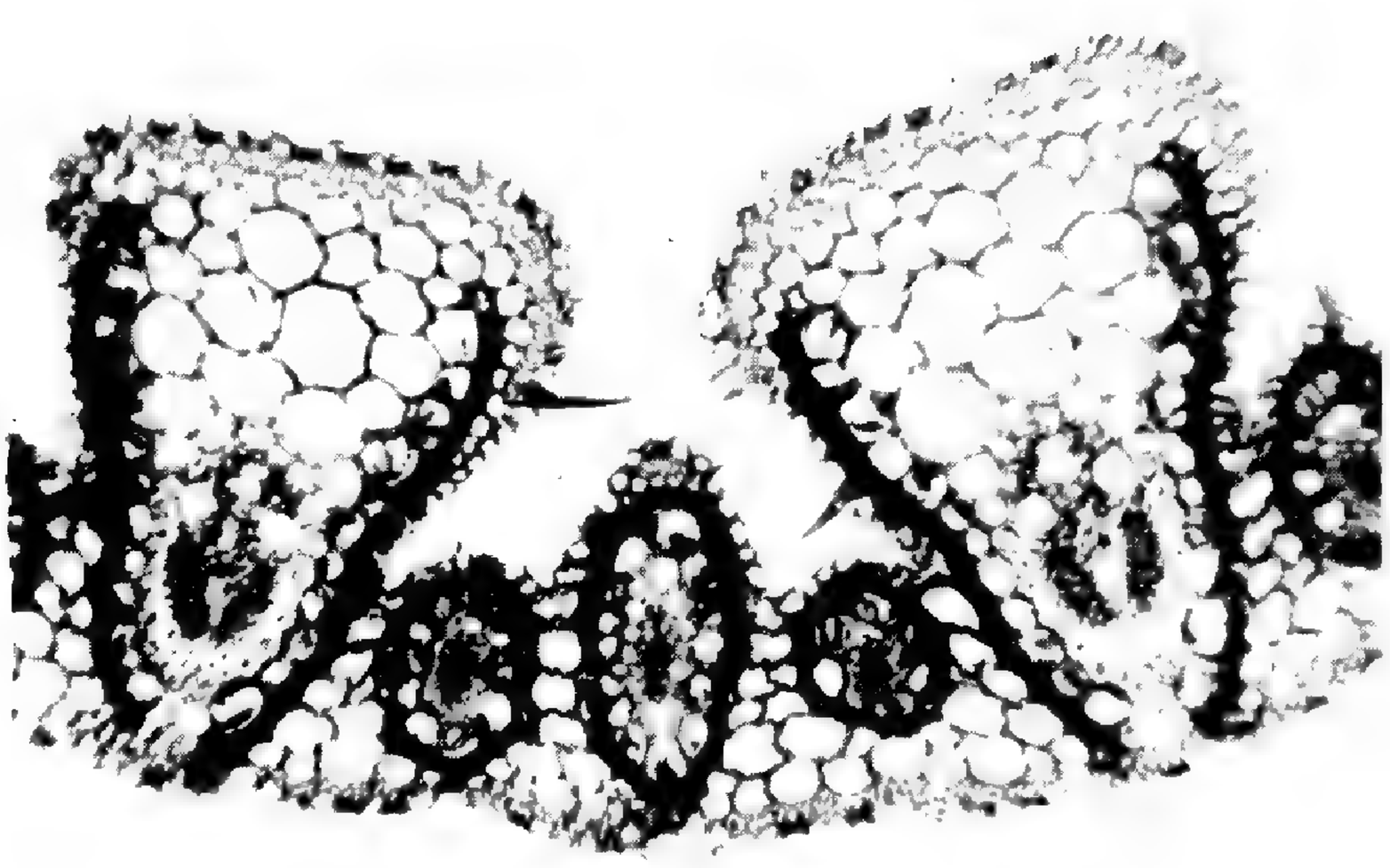
Anatomical structures of the leaves of Muhlenbergias, subgenus *Podosemum:* FIG. 1.—*Muhlenbergia lindheimeri*, cross section through central part of leaf, showing heavily sclerified central unit and mass of thick-walled parenchyma of keel (*Burr* 513), ×50. FIG. 2.—*M. lindheimeri*, cross section through lateral part of leaf, showing two 1° and two 2° units (*Burr* 513), ×134. FIG. 3.—*M. palmeri*, cross section through central part of leaf, including two 1° units and, between them, one 2° and two 3° units (*Pringle* 1417), ×134. Abbreviations: par=parenchyma (thick-walled); s=sclerenchyma; ch=chlorenchyma sheath (mesophyll); bc=bulliform cells; os=outer sheath; cc=colorless cells; is=inner sheath; x=xylem; ph=phloem (line points to darkstained, active, nonsclerosed portion).



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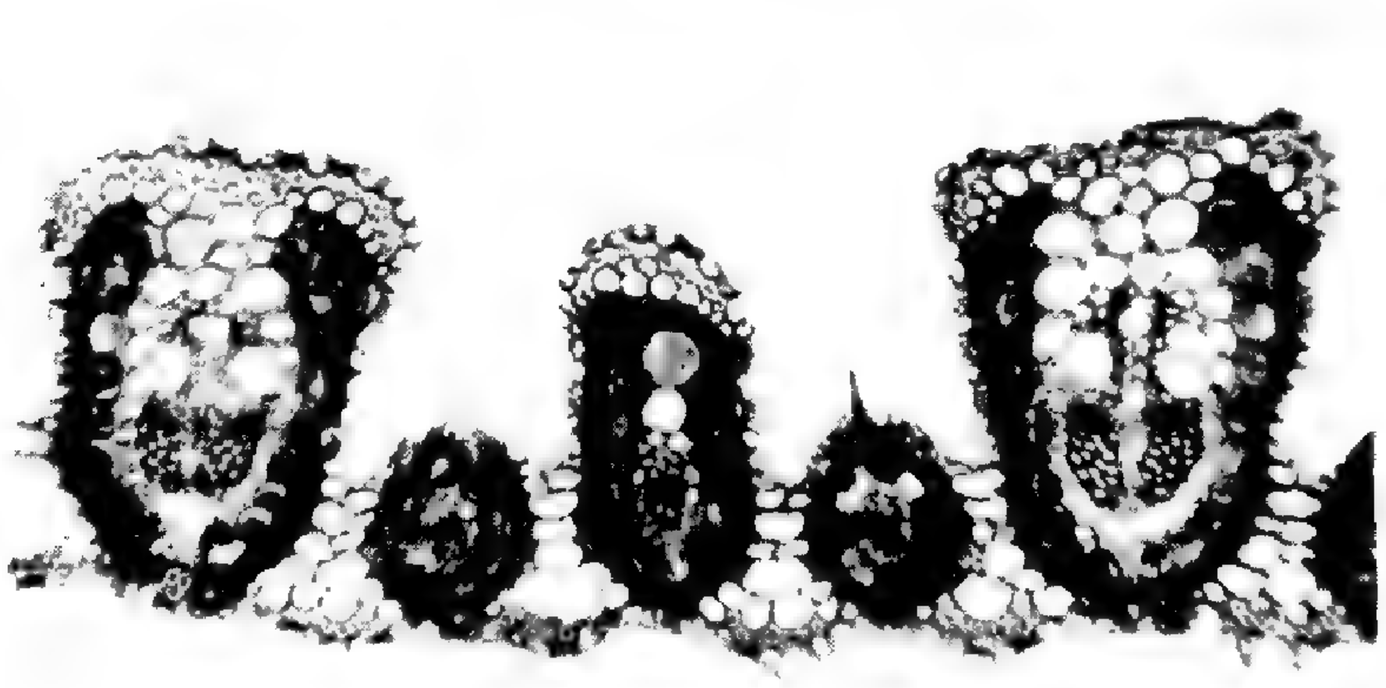

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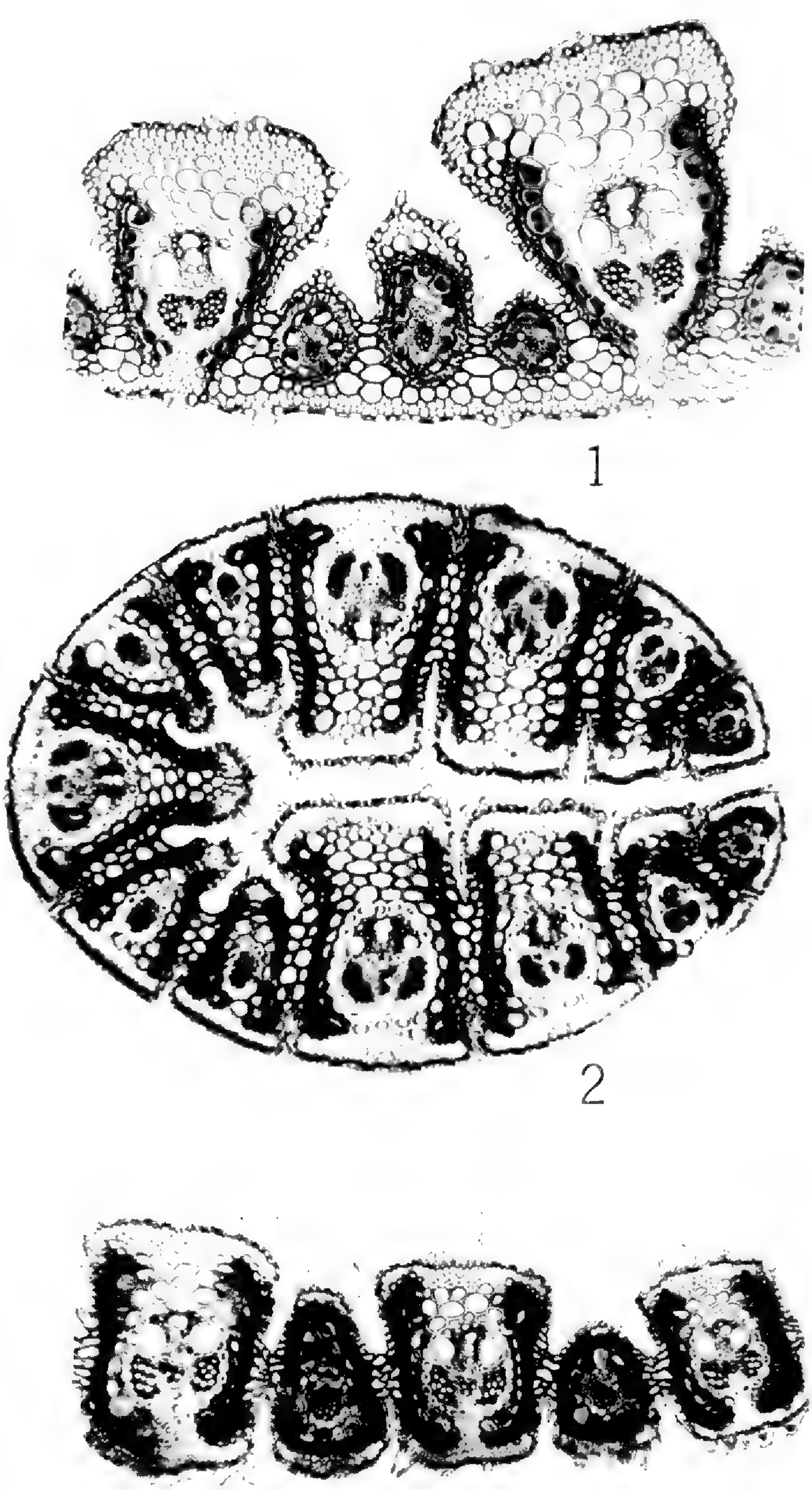
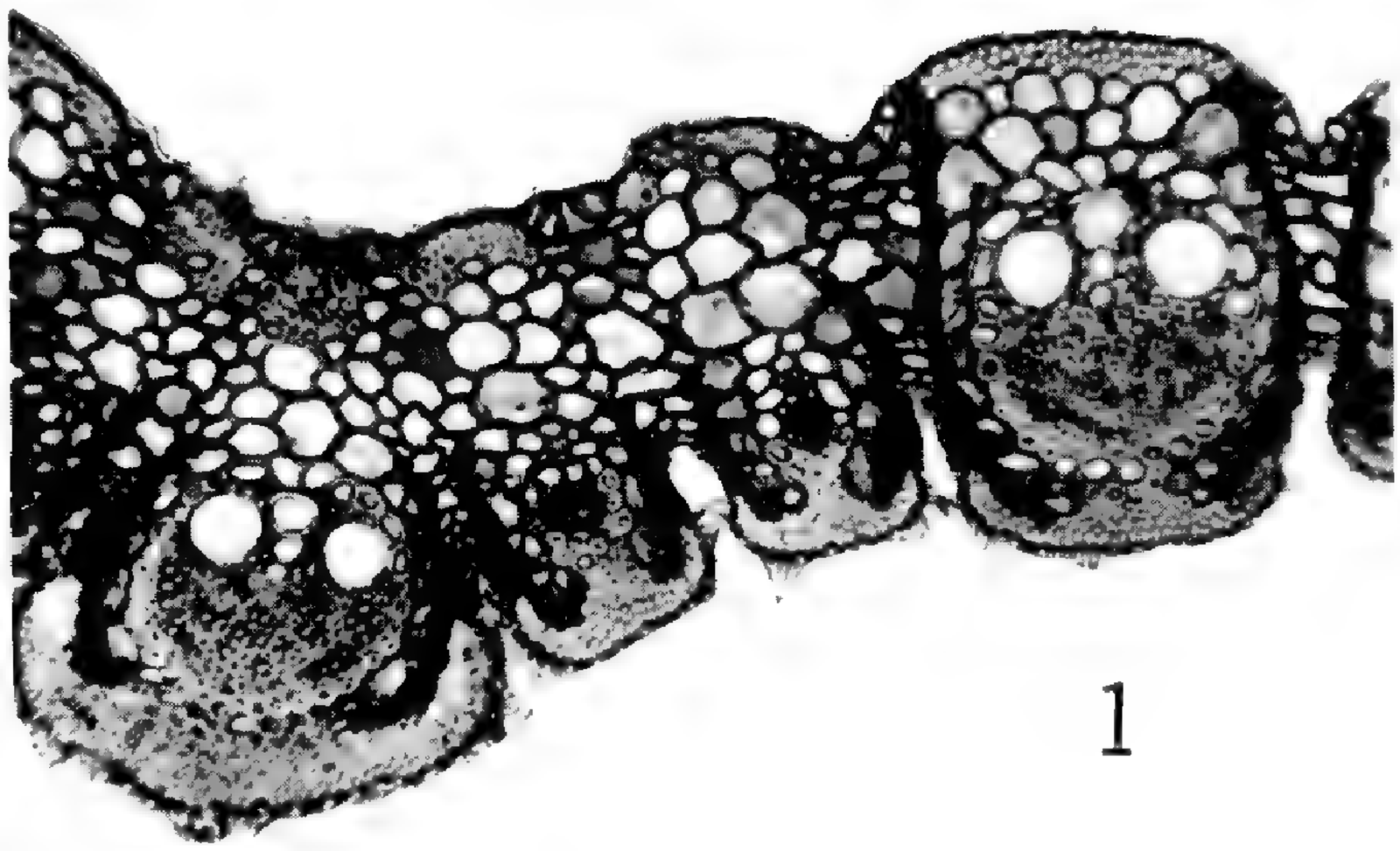
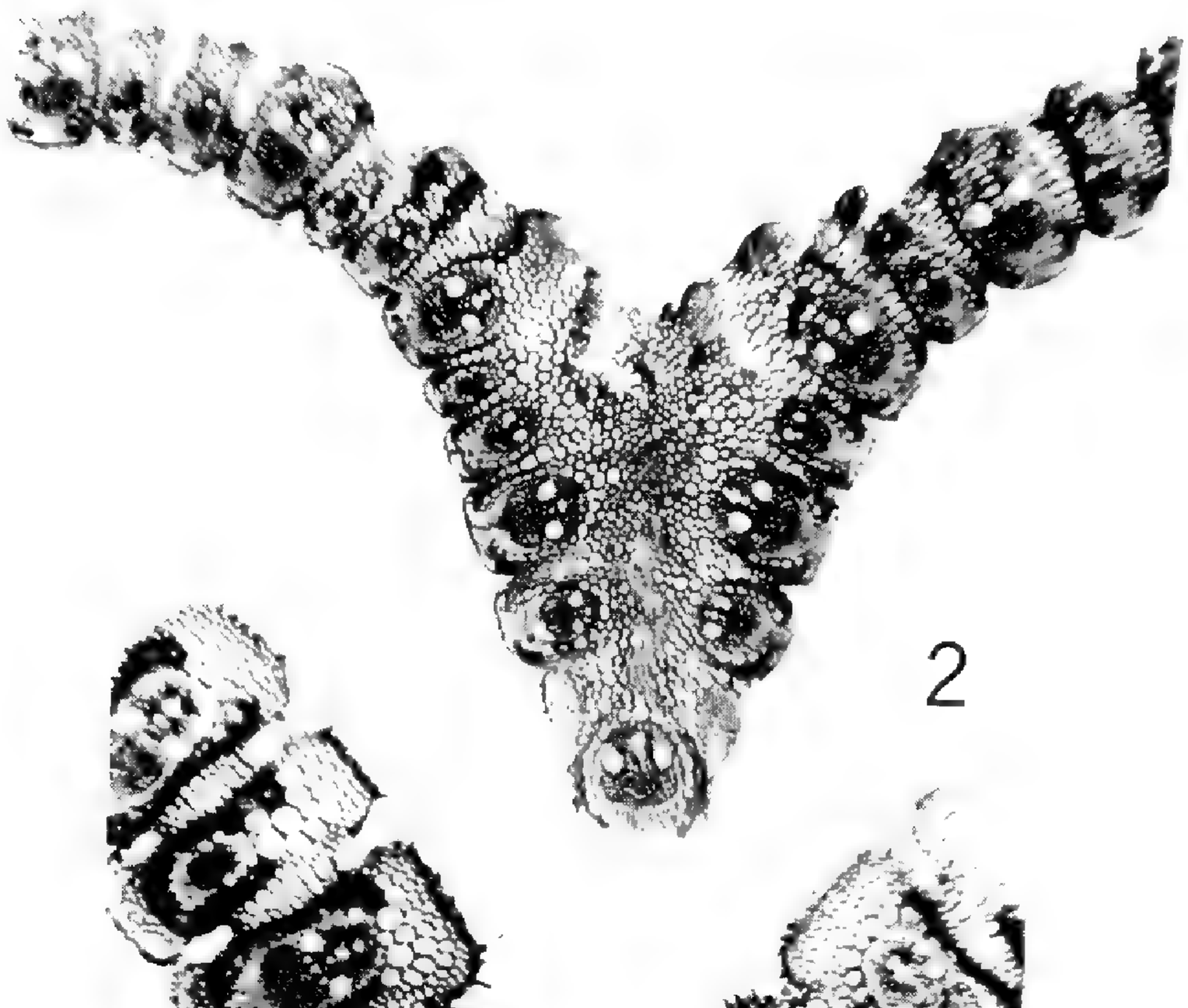
Photomicrographs of leaf cross sections: FIG. 1.—*Muhlenbergia rigens*, young innovation leaf, between ligule and point 2.5 cm. from ligule on blade (*Soderstrom* 731), ×187. FIG. 2.—*M. rigens*, culm leaf, between ligule and point 1 cm. from ligule on blade (*Reeder & Reeder* 2662), ×150. FIG. 3.—*M. dubia* (*Soderstrom* 509), ×150.

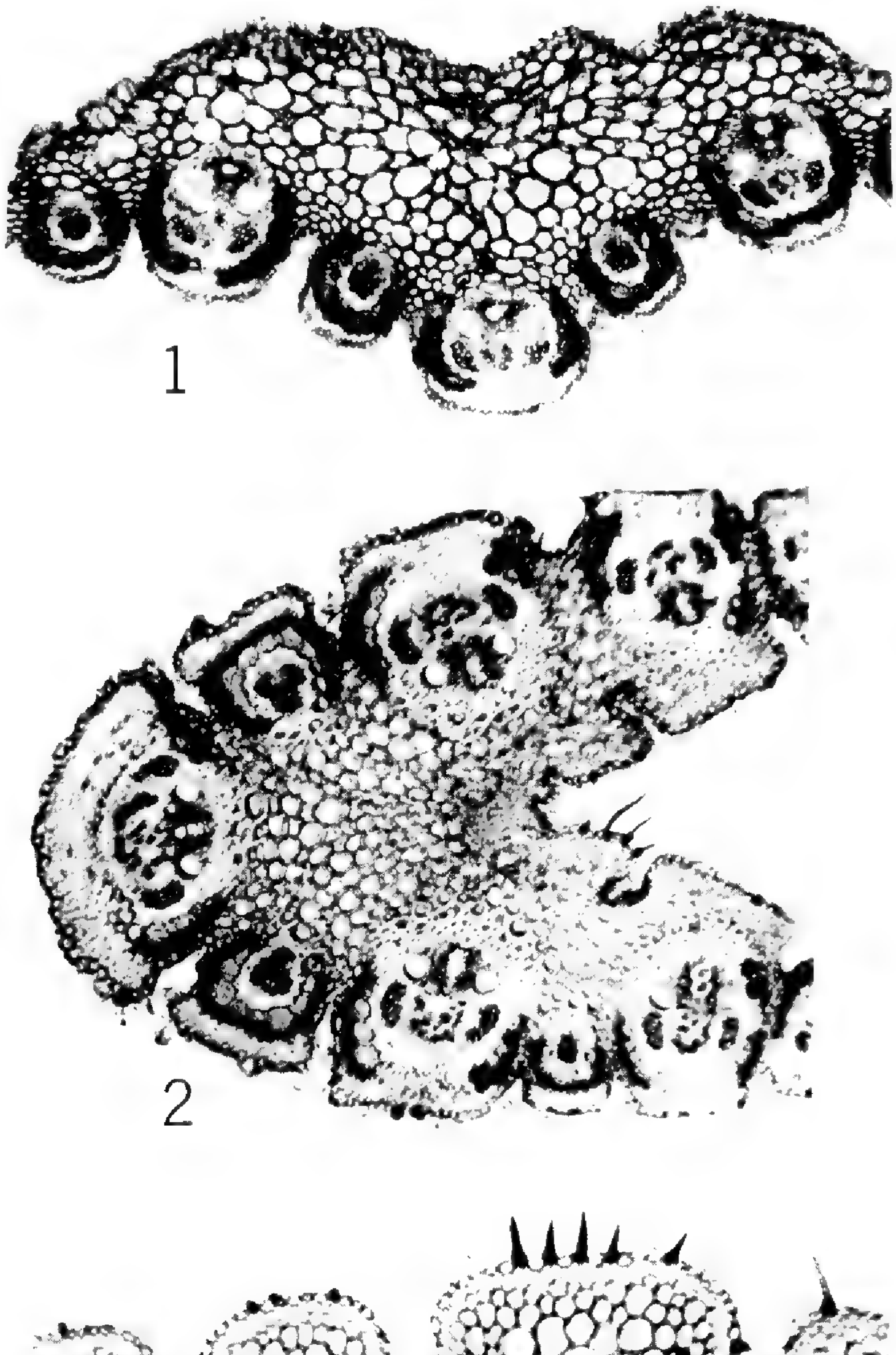


Photomicrographs of leaf cross sections: FIG. 1. —*Muhlenbergia palmeri* (*Pringle* 1417), ×194. FIG. 2.—*M. expansa* (*Amer. Gr. Nat. Herb.* 1374), ×156. FIG. 3.—*M. holwayorum* (*Rusby* 201), ×156.

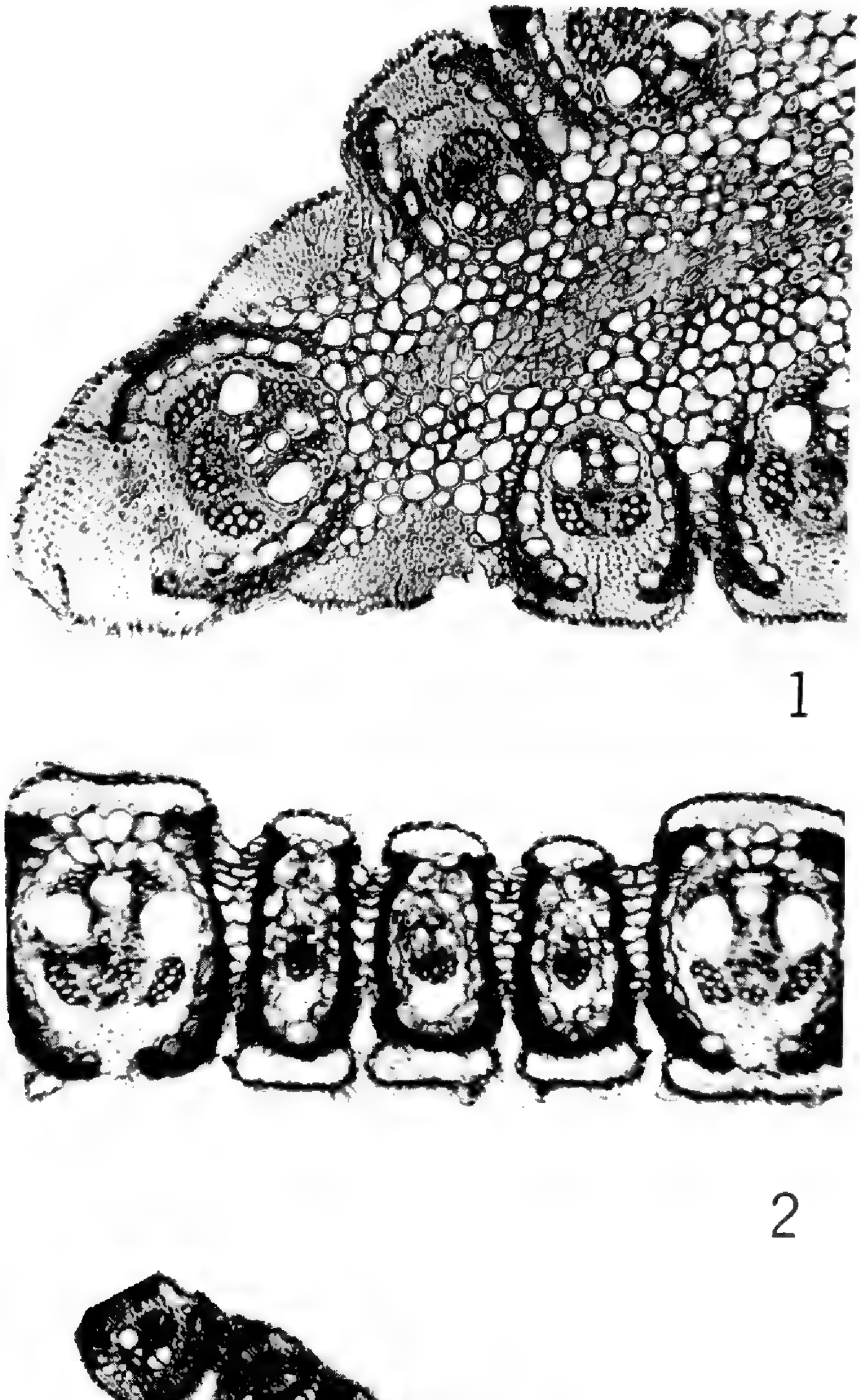




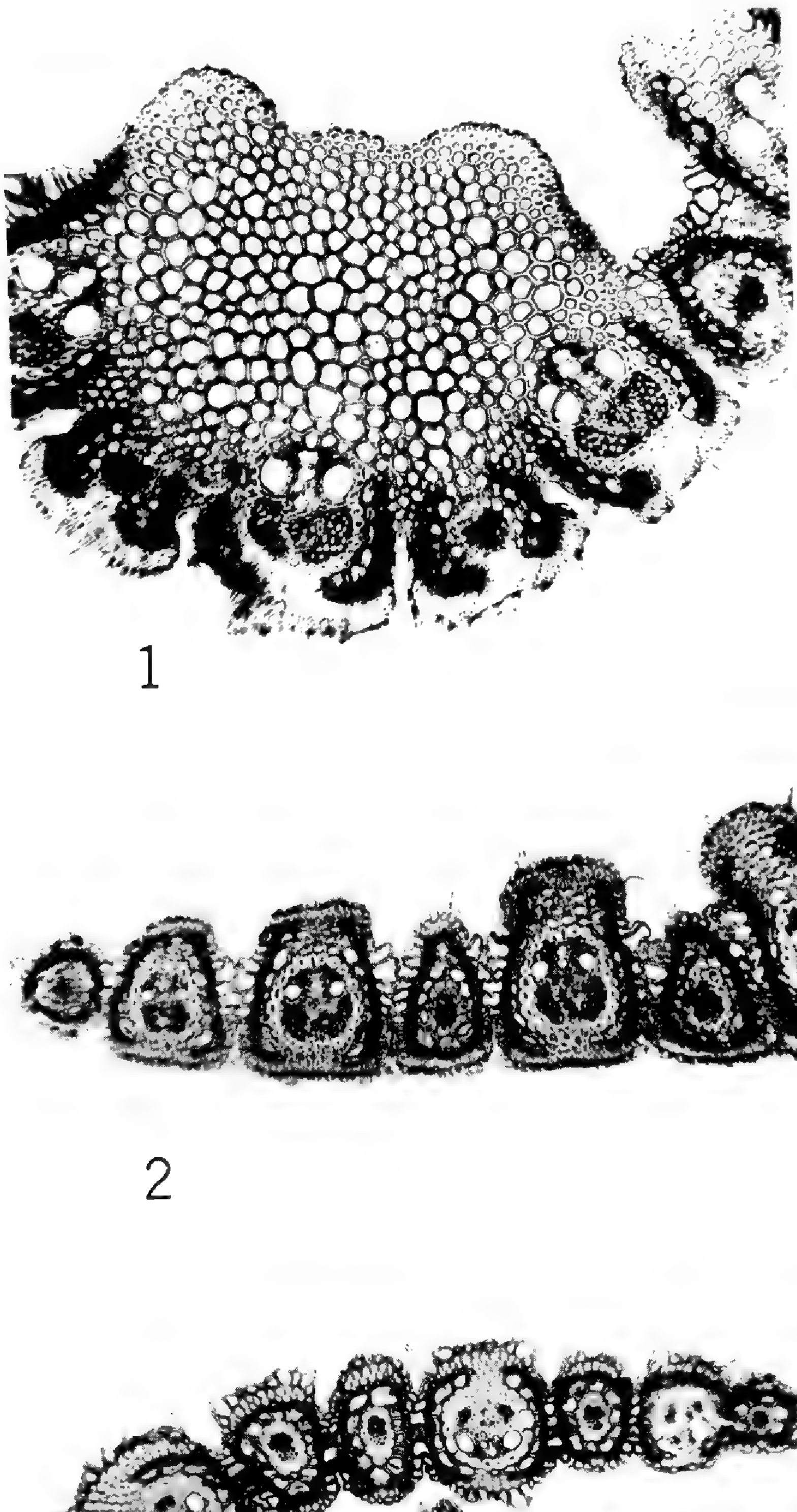
Photomicrographs of leaf cross sections: FIG. 1.—*Muhlenbergia macrotis* (*Mexia* 9098), ×165. FIG. 2.—*M. gigantea* (*Soderstrom* 607), ×58. FIG. 3.—*M. lindheimeri* (*Burr* 513), ×77 (cf. pl. 8, fig. 3).



Photomicrographs of leaf cross sections: FIG. 1.—*Muhlenbergia breviligula* (*Standley* 76731), ×165. FIG. 2.—*M. involuta* (*Silveus* 780), ×165. FIG. 3.—*M. lindheimeri* (*Burr* 513), ×206 (cf. pl. 7, fig. 3).



Photomicrographs of leaf cross sections: FIG. 1.—*Muhlenbergia gigantea*, showing keel (*Soderstrom* 607), ×165. FIG. 2.—*M. robusta* (*Reeder & Reeder* 2128), ×165. FIG. 3.—*M. torreyana* (*Bissell*), ×165.



Photomicrographs of leaf cross sections: FIG. 1.—*Muhlenbergia longiligula* (*Blumer* 1424), ×165. FIG. 2. *M. capillaris* (*Silveus* 2396), ×165. FIG. 3.—*M. longiglumis* (*Pringle* 2365), ×165.

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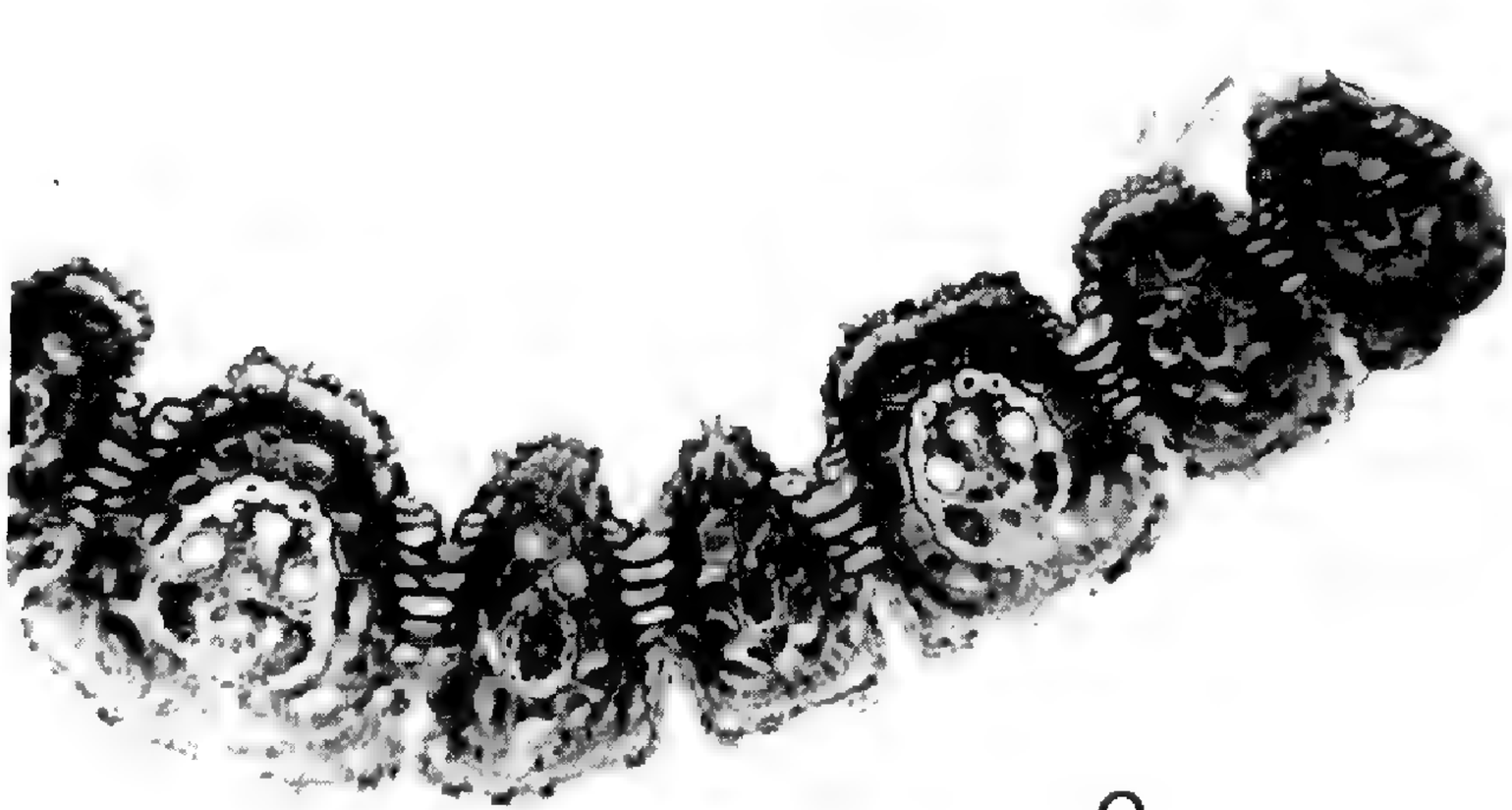

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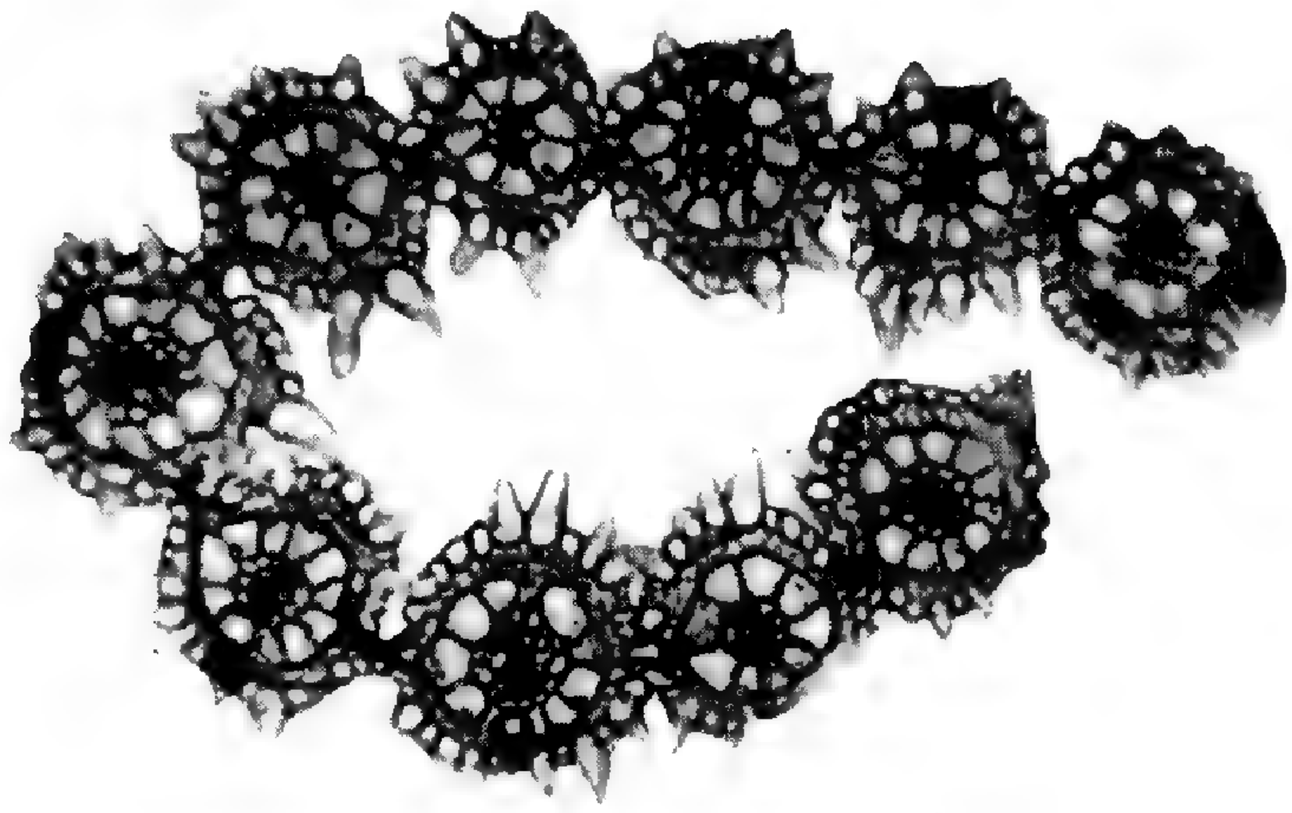
Photomicrographs of leaf cross sections: FIG. 1.—*Muhlenbergia reverchoni* (*Silveus* 2478), × 165. FIG. 2.—*M. elongata* (*Pringle* 938), ×165. FIG. 3.—*Muhlenbergia* aff. *montana* (*Reeder & Reeder* 2572), ×165.



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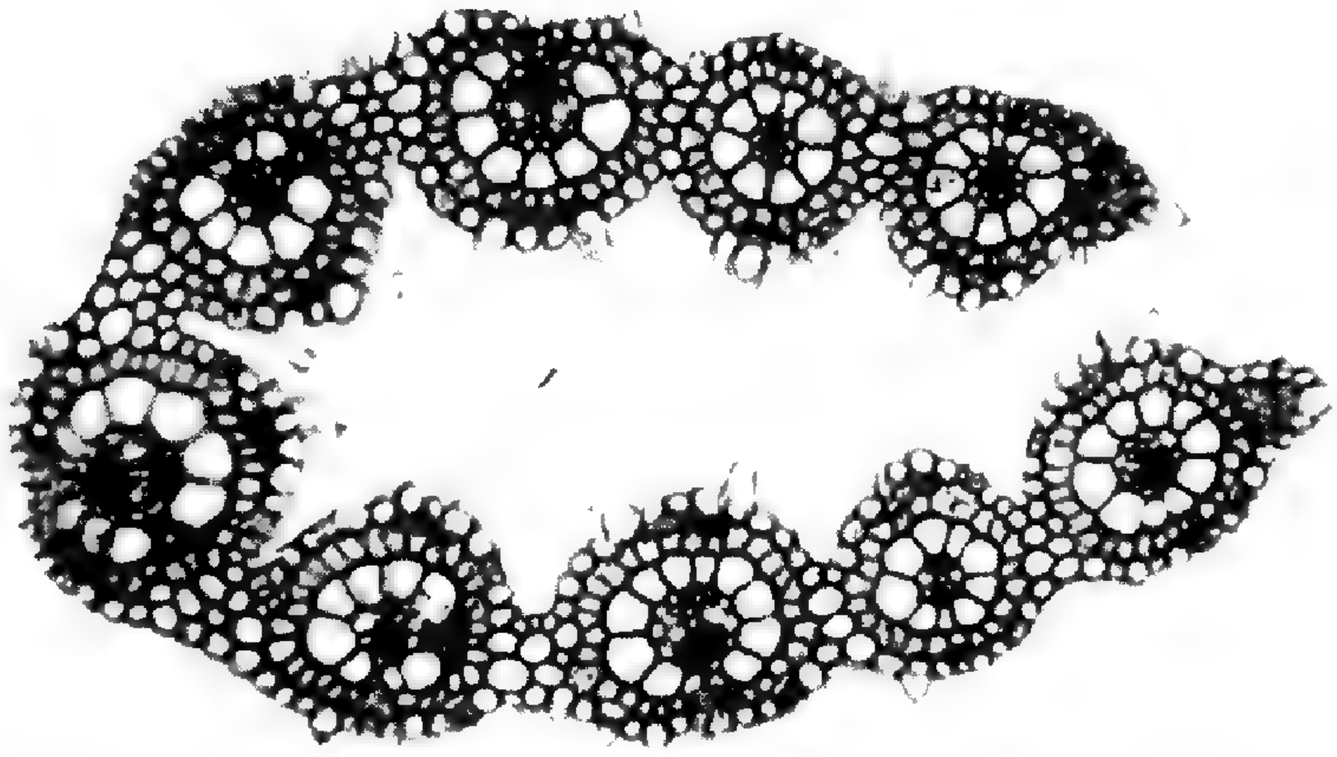

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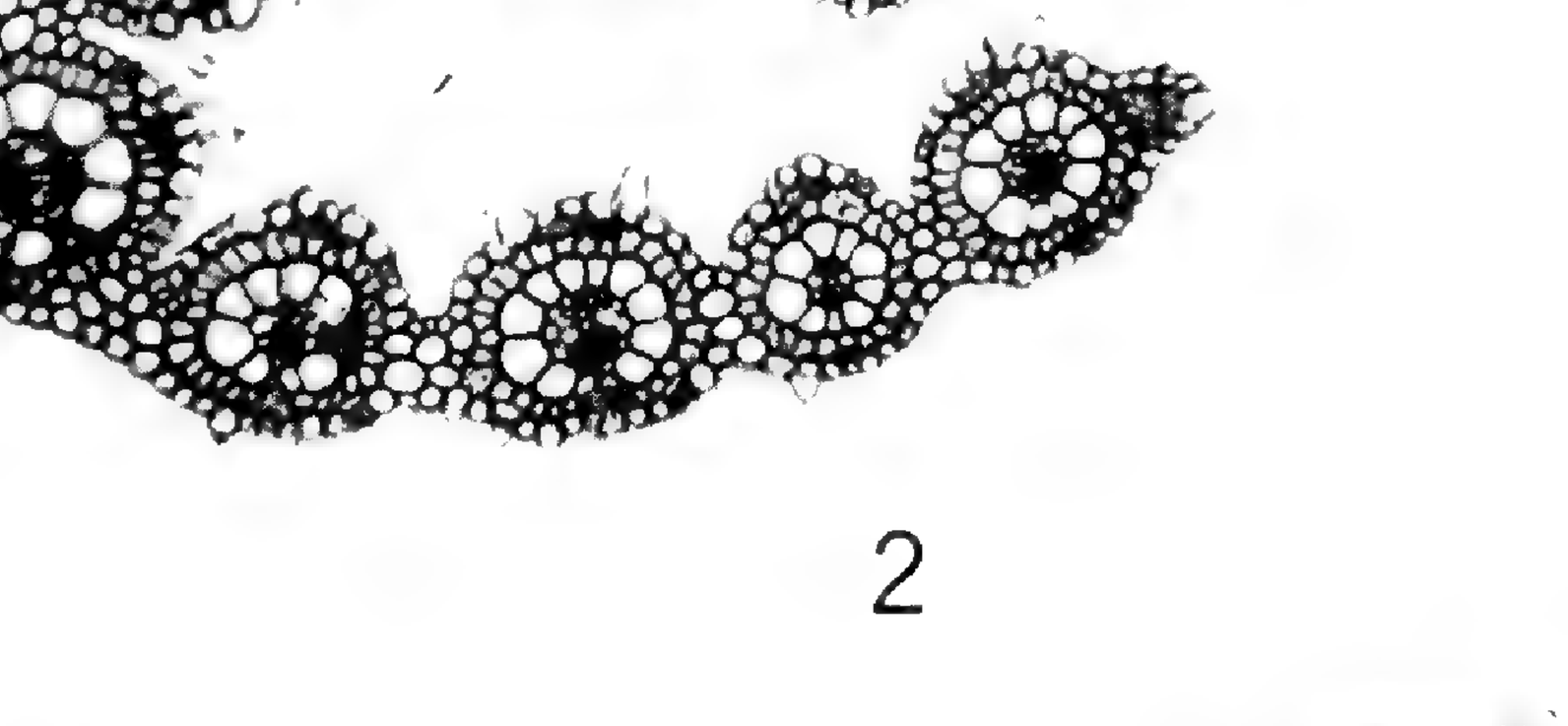

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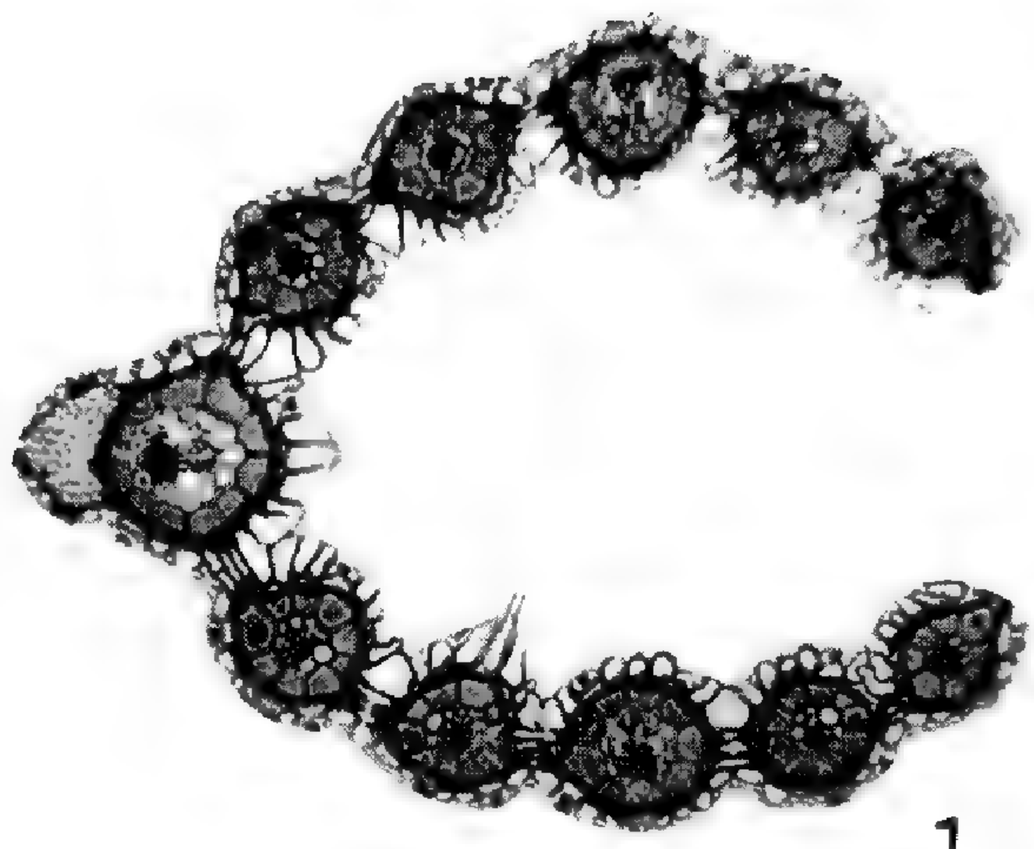
Photomicrographs of leaf cross sections: FIG. 1.—*Muhlenbergia peruviana* (*Pearson* 1), ×165. FIG. 2.—*M. pulcherrima* (*Reeder & Reeder* 2535), ×165. FIG. 3.—*M. arizonica* (*Reeder & Reeder* 2602), ×165.



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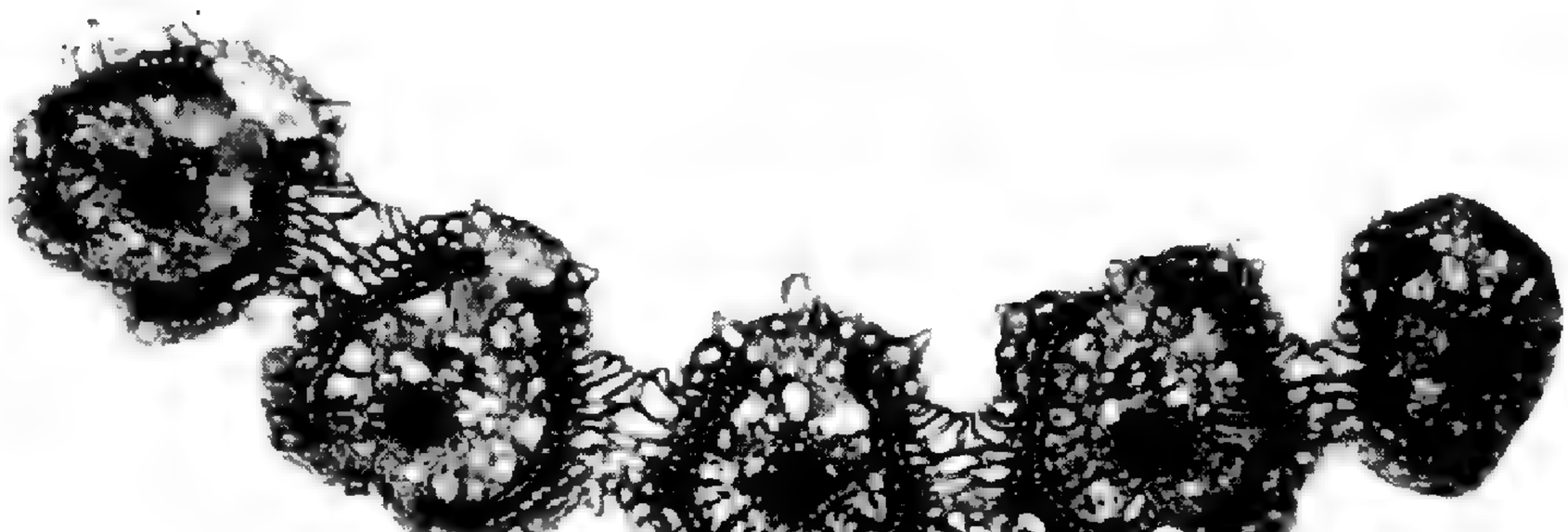

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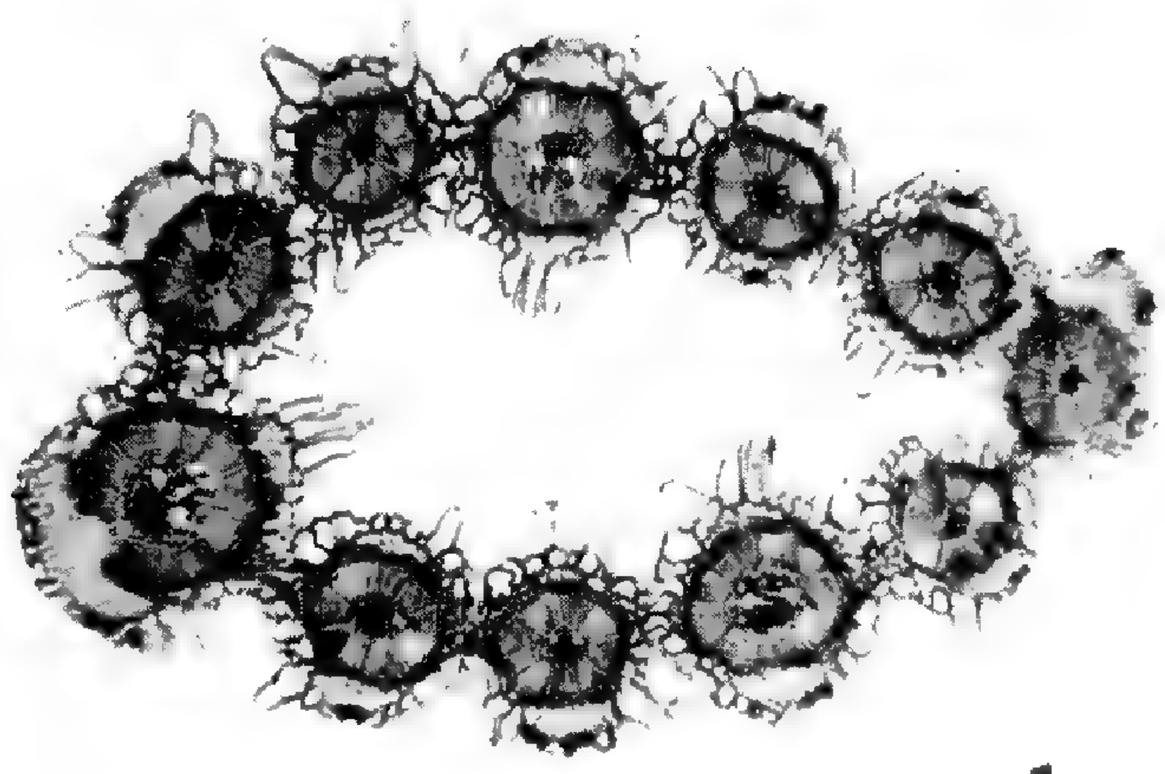
Photomicrographs of leaf cross sections: FIG. 1.—*Muhlenbergia confusa* (*Reeder & Reeder* 2684), ×165. FIG. 2.—*M. richardsonis* (*Goodding* M–3272), ×206. FIG. 3.—*M. plumbea* (*Reeder & Reeder 2218*), ×165.



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Photomicrographs of leaf cross sections: FIG. 1.—*Muhlenbergia crispiseta* (*Reeder & Reeder* 2545), ×165. FIG. 2.—*M. asperifolia* (*Hardies* M-103), ×165. FIG. 3.—*M. uniflora* (*Johnson*), ×206.

BULLETIN OF THE UNITED STATES NATIONAL MUSEUM

CONTRIBUTIONS FROM THE UNITED STATES NATIONAL HERBARIUM

VOLUME 34, PART 5

THE GENUS MELOCHIA L. (STERCULIACEAE)

By AARON GOLDBERG

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THE GENUS MELOCHIA L. (STERCULIACEAE)

By Aaron Goldberg

History of the Genus

Linnaeus validated the name *Melochia* by including it in the first edition of his Species Plantarum (37). In his Genera Plantarum (38) of the following year under the description of *Melochia* he cited only Dillenius (9), who had described and illustrated only *Melochia corchorifolia* in the genus *Melochia*. According to the current International Code of Botanical Nomenclature (33), it is agreed to associate generic names which appear in Linnaeus' Species Plantarum, edition 1, 1753, with the first subsequent description given under those names in Linnaeus' Genera Plantarum, edition 5, 1754. Therefore, *Melochia corchorifolia* L. is considered to be the type species of the genus.

Melochia is a name altered from the Arabic name of *Corchorus olitorius* L., a salad plant in the East, and according to Gray (20) the name was borrowed by the Arabs, through the Syriac, from the Greek word for the mallow.

Several genera have been published and subsequently reduced to synonymy under *Melochia*. In 1777 Houttuyn (27) introduced the name *Visenia* for his *V. umbellata*, a common tree of southeastern Asia and the Pacific Islands. In 1854 Gray (19) expressed the opinion that *Visenia* could not be generically distinguished from *Melochia*. In 1895 Schumann (48) gave it its present status as a section of *Melochia*.

In 1787 Medicus (42) introduced the name *Moluchia* for species with pyramidal fruits—placed in the section *Pyramis* in this paper. In 1803 Ventenat (64) introduced the name *Riedlea*, characterized by a 5-valved globular capsule, filaments united in a column, and a calyx subtended by 3 bracts. *Riedlea* is placed in the section *Melochia* in this paper. In 1823 Humboldt, Bonpland, and Kunth (28) introduced *Mougeotia* for species with a pentacoccic capsule. DeCandolle (8) reserved the name *Melochia* for species placed in the section *Pyramis* in this paper, and used the name *Riedleia* for *Riedlea* Vent., *Mougeotia* H. B. K., and *Visenia* Houtt. He also established the tribe Hermannieae, which includes *Hermannia* L., *Melochia* L., and *Waltheria* L. Two years later Sprengel (51) used *Melochia* as did DeCandolle, but substituted *Visenia* for *Riedleia*, probably on the basis of priority.

In 1825 St.-Hilaire (46) reported on his rather extensive collections of *Melochia* in southern Brazil, and gave reasons for not considering *Riedlea* Vent. generically distinct from *Melochia*. He mentioned that the flowers are very similar and that, as a rule, other characters being the same, Linnaeus would not divide a genus if the flowers were the same but the fruits different. He did not consider the presence of bracts subtending the calyx a generic character and pointed out that there are intermediate forms in the types of dehiscence of the fruit in *Melochia* and *Riedlea*.

In 1836 Presl (45) introduced *Physodium*, and mentioned that it differed from *Riedleia* in having an inflated, closed calyx, linear anthers, and an acute-angled, stipitate capsule. Bentham and Hooker (3) maintained *Melochia* and *Physodium*, but, considering St.-Hilaire's observations and their own, they placed *Riedlea* in synonymy. Hemsley (25) did not consider *Physodium* to be generically distinct from *Melochia* but followed Bentham and Hooker in maintaining it.

In 1854 Triana and Karsten *in* Triana (58) introduced *Anamorpha*, and in 1858 Turczaninow (60) introduced *Physocodon*. Both have since been reduced to *Melochia*. They contain species now placed in the section *Mougeotia*.

In 1864 Grisebach (22) divided the genus into the sections *Eumelochia*, *Riedleia*, and *Mougeotia*. As emended in description, and as changed in nomenclature, in accord with the International Code of Botanical Nomenclature, these sections are maintained in the present paper.

Schumann (47), in the next major treatment of the genus, considered all of the genera mentioned above, occurring in Brazil, to be synonyms of *Melochia*, and he accepted Grisebach's sectional division of the genus.

In 1890 Garcke (17) discussed part of the extensive synonymy in the genus.

In 1895 Schumann (48), in treating *Melochia*, added *Visenia* as a section containing certain species of Asia and the Pacific Islands, and reduced *Physodium* to synonymy.

In 1908 Fries (15) presented his concepts of the taxa in *Melochia* in South America. He examined and cited specimens from several European herbaria.

From time to time species and infraspecific taxa have been described in the genus *Melochia* and its synonyms. These are considered in the systematic section of this paper. Approximately 379 names and combinations have been used to describe the types of *Melochia*. Many are synonyms and many of the descriptions are very inadequate. I have made more than 30,000 observations of characters in the genus. About half of them were measurements under the dissecting micro-

scope. Thus, I have supplemented the information in the old descriptions. As a result of my studies, I consider 68 taxa to be adequate to describe the entities in the genus. Two new species are described and *Physodium* is placed in sectional status.

Division of the genus into several genera has been based on characters which show a gradual transition between species from section to section as follows: (1) The carpels of some species of the section *Mougeotia* have an obtusely rounded dorsal surface; in others the carpels are somewhat carinate in the distal half of the fruit and transitional to the section *Pyramis*. (2) In the size of the fruit from the section *Mougeotia* to the section *Pyramis*. (3) One type of dehiscence to another occurs between species. (4) The gradual change in degree of accrescence of the calyx, degree of union of the filaments, and length of the stipe. (5) In the size of bracts in all species and in the length of the internode between each of them and between them and the calyx.

In addition to the taxonomic treatments already mentioned, several floras and lists have been published in which pertinent *Melochia* are presented. Included among the regions treated are Mexico (52), several countries of Central America (25, 53, 54, 55, 56), several of the islands of the West Indies (4, 13, 22, 36, 62), Surinam (61), French Guiana (35), Venezuela (44), Colombia (59), Peru (39), Bolivia (14), tropical West Africa (29), Congo (18), Angola (11), the basin of the Zambesi River (12), Madagascar (1), India (26), Indochina (16, 57), Java (2), the Philippine Islands (43), and Fiji (49). Since the taxa attributed to the various regions by the authors of these floras and by me differ in some cases, I am including tables showing the distribution of the species of *Melochia* by countries (pp. 196 and 197).

Economic Importance

The genus *Melochia* has no outstanding economic importance. Some species, such as *M. pyramidata*, have fine silky fibers, but at present these are used only locally. Some species occur in pasture lands, especially savannas. Gentry mentioned (his specimen no. 943M [MICH]) that burros are very fond of the plant (*M. tomentella*). A few species are weeds in cultivated fields. The plants have a mucilaginous constituent that is used locally as a demulcent in enteritis due to dysentery. They are also used locally as a salad plant, and for smoking. The flowers are a source of food for honeybees.

Melochia umbellata (Houtt.) Stapf, a rapidly growing species of southern Asia and the Pacific Islands, is commonly planted as a shade tree in that part of the world.

Geographic Distribution

In America, *Melochia* is distributed over more than 5.6 million square miles. It ranges from approximately 33° N. to 33° S. latitude on the east coast, and from approximately 29° N. to 12° S. latitude on the west coast. The distribution of the genus in South and North America is shown in figures 1 and 2, respectively. The coordinates

FIGURE 1.—Distribution of *Melochia* in South America.

of many of the localities of the specimens studied were determined from the "Index to the Map of Hispanic America" (31).

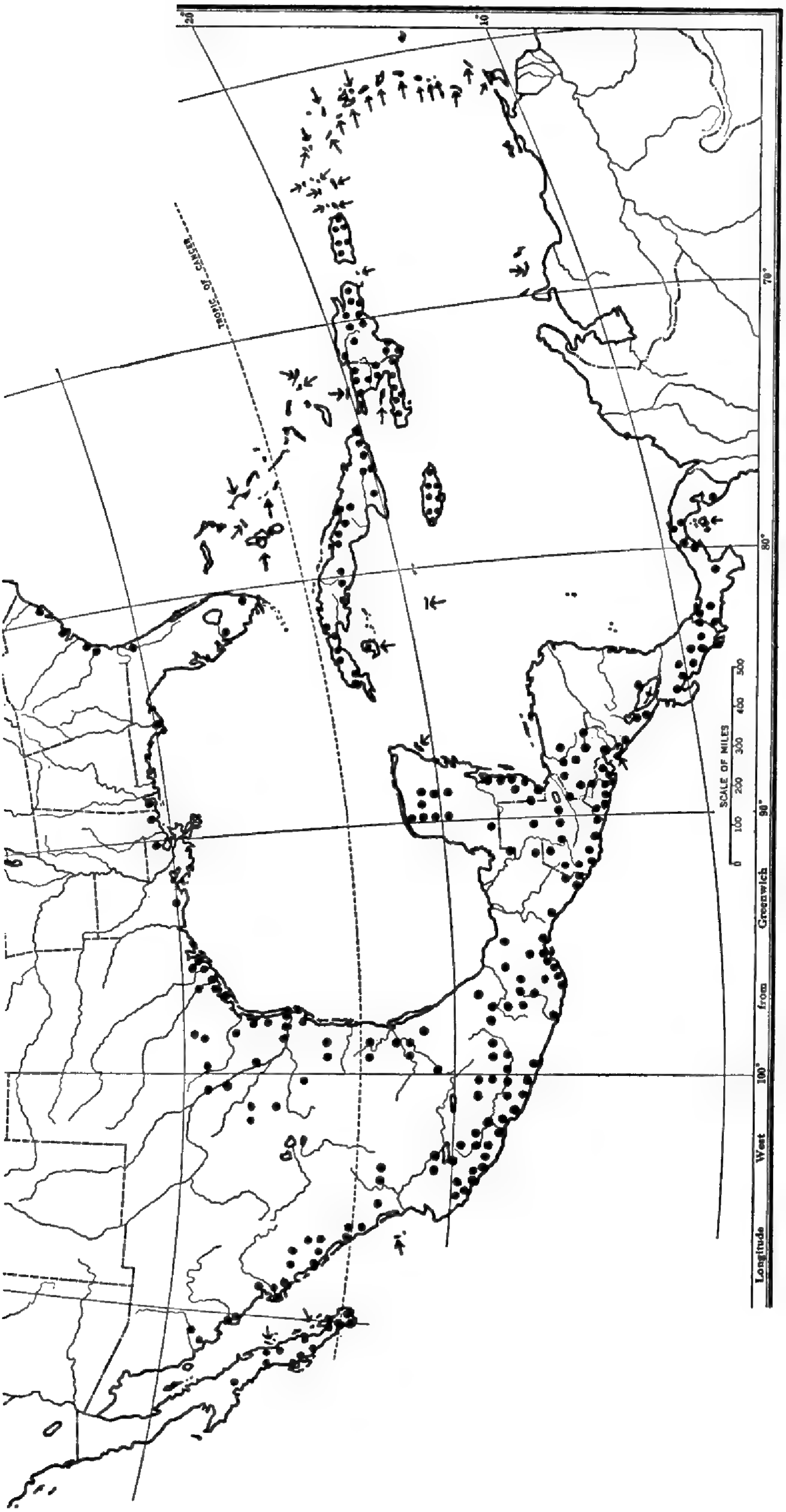

FIGURE 2.—Distribution of *Melochia* in North America.

TABLE 1.—*Distribution of American Species of* Melochia *by Countries*

MELOCHIA	United States	Mexico	Guatemala	British Honduras	Honduras	Salvador	Nicaragua	Costa Rica	Panama	Bahamas	Cuba	Hispaniola	Jamaica	Puerto Rico	Lesser Antilles	Trinidad-Tobago	French Guiana	Surinam	British Guiana	Venezuela	Colombia	Ecuador	Peru	Bolivia	North Brazil	South Brazil	Uruguay	Paraguay	Argentina
adenodes		X																											
anomala																			X	X	X			X	X			X	X
arenosa											X								X	X	X				X			X	
argentina		X	X			X																		X				X	X
bernoulliana																									X				
betonicifolia																				X	X				X				
caracasana																							X		X				
chamaedrys																									X				
colombiana																					X								
corchorifolia *	X							X																	X				
corymbosa		X																											
crenata													X								X								
gardneri																									X				
graminifolia																			X	X	X			X	X	X		X	
hassleriana																										X		X	
hermannioides																								X				X	X
illicioides																									X				
kerriifolia		X																		X	X				X	X			
lanata																									X	X			
lanceolata																			X	X									
leucantha																													
lupulina		X	X	X	X		X	X			X									X	X	X	X						
manducata		X	X					X		X	X										X	X			X				
melissifolia				X			X	X										X	X	X					X				
mollis																				X	X	X	X	X					
morongii																									X	X			
nodiflora		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X				X	X				X	X			
nudiflora		X	X		X			X																					
parvifolia											X								X	X	X				X			X	X
pilosa		X										X								X	X	X	X	X		X	X	X	X
pyramidata	X	X	X	X	X	X	X	X		X	X	X	X	X	X					X	X	X	X	X	X	X	X	X	X
rhodocalyx		X																											
savannarum											X																		
simplex																			X					X	X	X		X	X
splendens																					X				X				
thymifolia																													
tomentella		X																											
tomentosa	X	X			X		X			X	X	X	X	X	X	X					X	X			X				
tragiifolia		X																											
ulmifolia																	X	X	X	X	X				X				
villosa	X	X	X	X	X	X	X	X	X		X	X	X	X		X	X	X	X	X	X	X	X	X	X	X		X	X
werdermannii																													

*Adventive.

The genus occurs in more than 6.7 million square miles of the Old World, from 37° N. in eastern Asia to 24° S. in the Pacific Islands, and from 18° N. to 16° S. in western Africa and 2° S. to 20° S. in eastern Africa. The distribution of the genus in Asia, the East Indies, and Africa is shown in figures 3, 4, and 5, respectively. The

TABLE 2.—*Distribution of Extra-American Species of* Melochia

MELOCHIA	Africa	Madagascar	Asia	East Indies, Philippines	New Guinea	Australia	Solomon Islands to New Caledonia	Fiji Islands	Samoa, Tonga & East Pacific	Caroline & Marianas
aristata									×	
bracteosa	×	×								
compacta										×
corchorifolia	×	×	×	×	×	×				×
degeneriana								×		
grayana								×		
lanceolata		×								
longepetiolata								×		
melissifolia	×									
mollipila								×		
odorata					×		×			
pyramidata *		×		×	×	×				
roseiflora								×		
tomentosa *		×								
umbellata			×	×	×					
villosissima										×
vitiensis								×		

* Adventive.

coordinates of many of the localities were determined from the Columbia Lippincott Gazetteer of the World (5).

Distribution of the various taxa is given in greater detail at the end of the respective descriptions. Distribution of species of *Melochia* by countries is also given in tables 1 and 2.

Thirty-nine species are considered to be endemic to America, one to southern Asia and the southwest Pacific islands, ten to the southwest Pacific islands, one to Africa, two to Africa and South America, and one to Asia, Africa, and the southwest Pacific islands.

Two American species occur as weeds in the Eastern Hemisphere and one species has been transported from the Eastern Hemisphere to America, perhaps as a weed seed in shipments of rice.

Some species occur in deserts with less than 10 inches of annual rainfall, others grow in tropical rain forest where the annual precipitation is 126 inches.

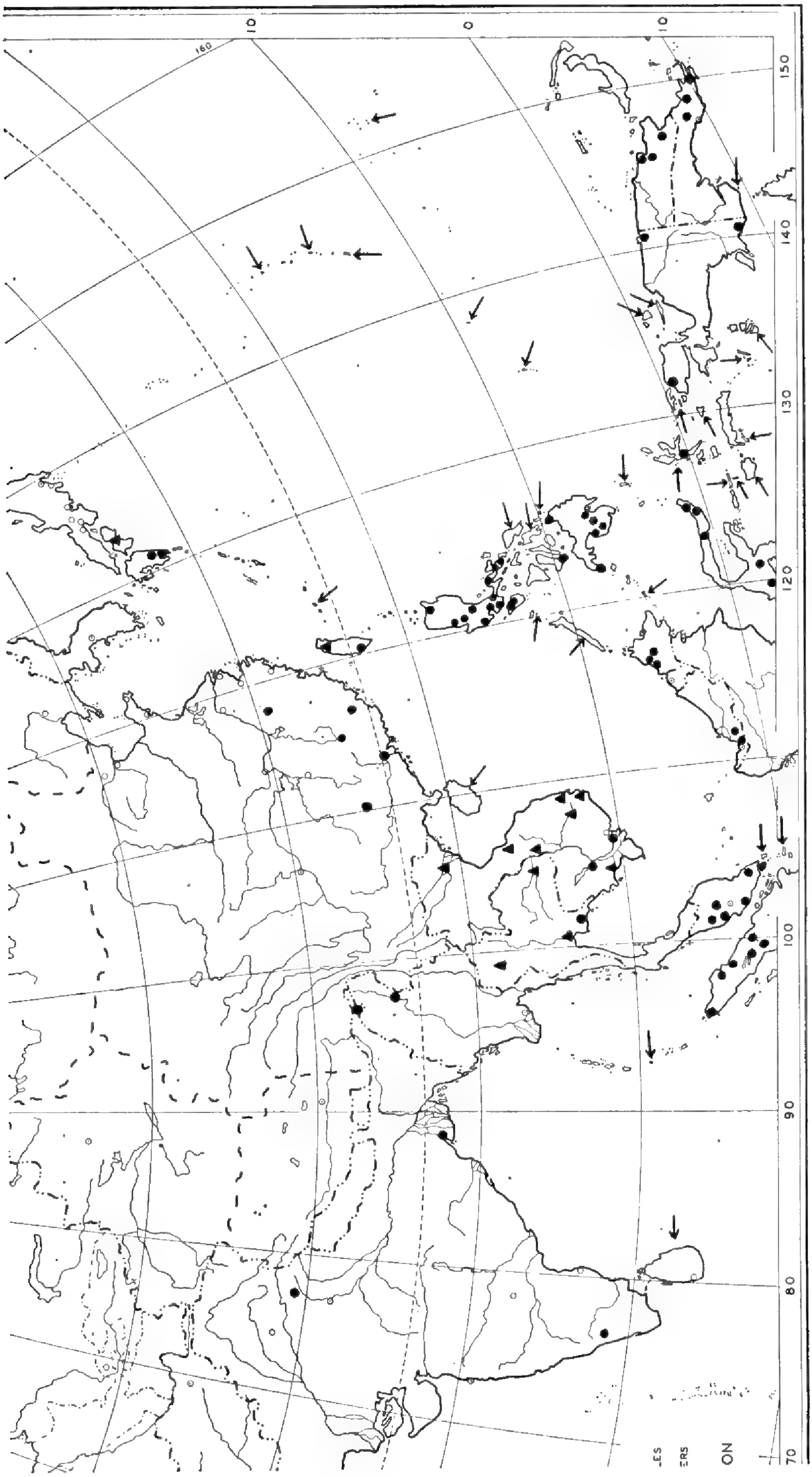

FIGURE 3.—Distribution of *Melochia* in Asia. *Melochia corchorifolia* is generally distributed in the hotter parts of India, from Kumaon to Sikkim, Malacca, and Ceylon [Hooker (26)].
●=cited in text ▲=from the literature

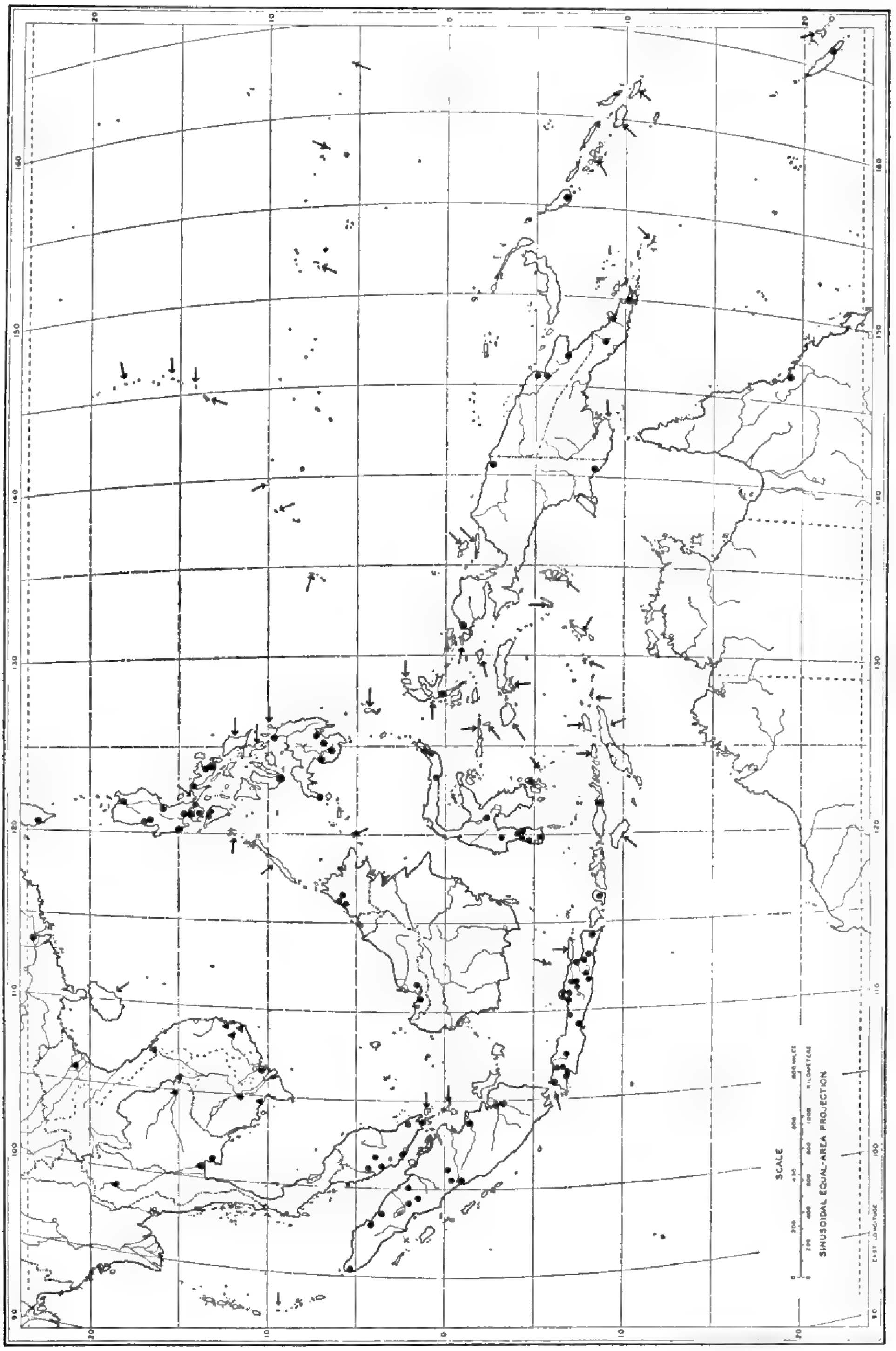

FIGURE 4.—Distribution of *Melochia* in the East Indies.
●=cited in text ▲=from the literature

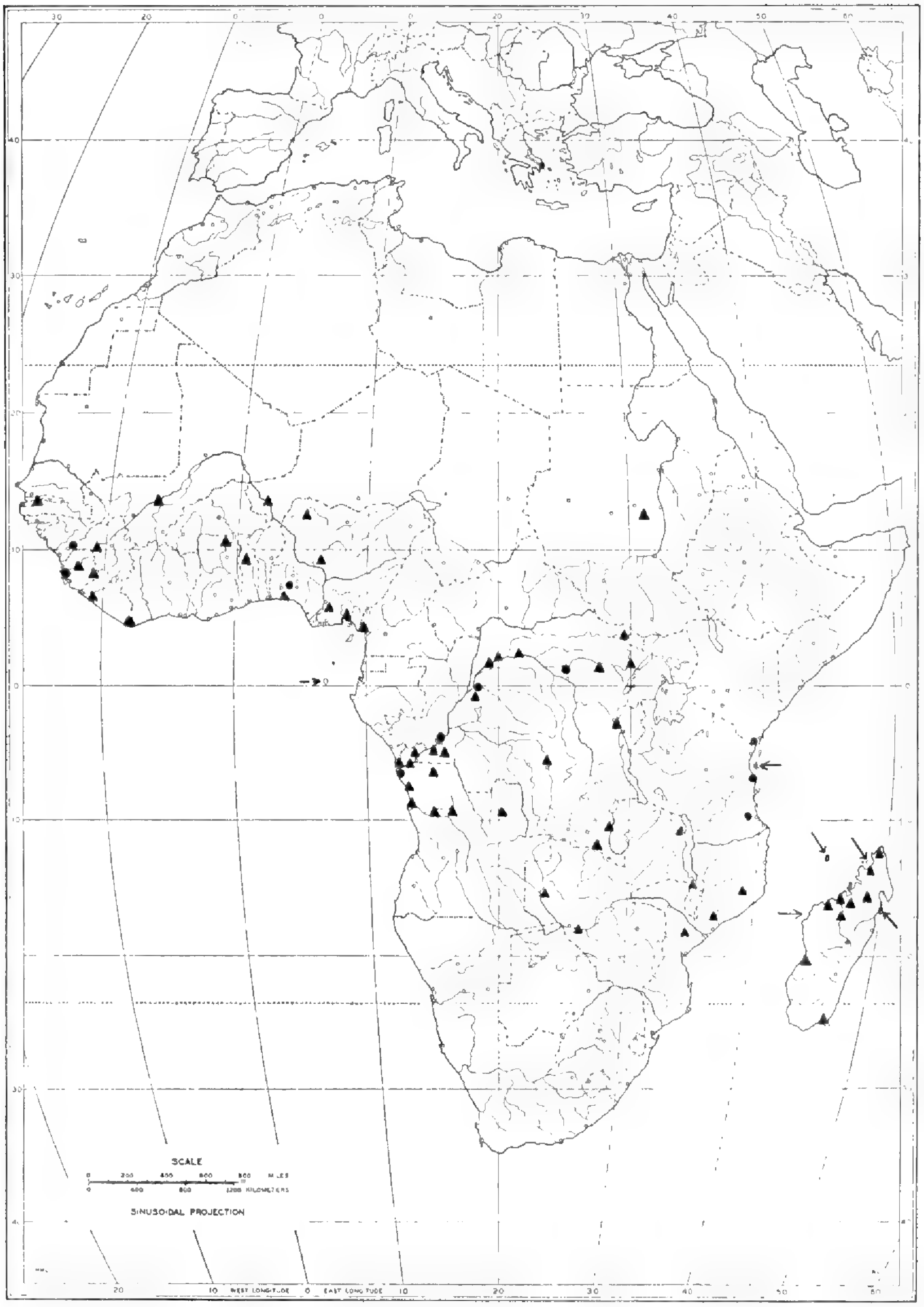

FIGURE 5.—Distribution of *Melochia* in Africa.

●=cited in text ▲=from the literature

Taxonomic Characteristics

Most species of *Melochia* are perennial shrubs or subshrubs; a few are herbs or small trees. A taproot is usually present, but secondary roots are often numerous. The young stems sometimes are hollow or

have a large pith and are often provided with small, round lenticels. They may be pubescent or glabrous. The bast fibers of the stem are tough.

Several kinds of hairs occur in the genus. They may be stellate, with 3 to 13 rays, forked, simple, or glandular. The last are several cells long, with the distal cell enlarged.

The leaves are simple and alternate and vary greatly in size, shape, and pubescence between species, sometimes within species. Their margins are usually irregularly crenate-serrate.

The inflorescences are axillary, terminal, leaf-opposed (the peduncle leaving the stem 180° from the insertion of the petiole at the same node), or 90° from the leaf insertion. They are cymose. The peduncle may be simple, branched, or absent. The bracts and stipules are usually similar in shape, size, and pubescence.

The flowers are polypetalous, actinomorphic, perfect, and hypogynous. They are sometimes matutinal and sometimes fragrant and visited by honeybees. They are usually dimorphic, the gynoecium and androecium differing in length in flowers of different plants of a species. The condition may be slight or marked. In figure 6, 1A, 1B, 3A, and 3B illustrate the longistylous condition, and 2A, 2B, 4C, and 4D the brevistylous condition.

The five fertile stamens are antepetalous, and the filaments are free of the petals or partially attached to them. The filaments are partially or completely attached to one another. Staminodes are usually absent; sometimes there are five, usually dentiform, alternate with the fertile stamens. The anthers are dithecous, extrorse, and attached to the filaments at the middle. The pollen is smooth, usually globular and 34–49μ in diameter. Sometimes, according to Erdtman (10), it is subprolate, and 51μ long and 44μ wide.

There are usually 5, rarely 6–8, carpels opposite the petals. The placentation is axile and the ovules are attached one-fourth to one-third the way up from the base of the carpel. The ovules are superposed and close to one another, and anatropous, with the funicle ascending on the adaxial surface of the ovule.

The calyx is campanulate, quinquefid, valvate in aestivation, and persistent. Sometimes glandular tissue is between the calyx and the corolla and between the bases of the petals.

The 5 petals are imbricate and contorted in aestivation and often marcescent. They are flat and veined.

The fruit may be subglobular, and more or less pentagonal (figure 6, 1D, 2D) or pyramidal and pentapterous (figure 6, 3C). A rostrum may be present (figure 6, 3C), or absent, or the apex of the capsule may be retuse (figure 6, 4E). A fairly long stipe may be present (figure 6, 4E) or it may be absent. Dehiscence of the fruit may be (1) septicidal

into cocci with a narrow ventral slit, (2) loculicidal all along the ventral suture, the cells gaping ventrally, and a fifth to half way along the dorsal suture, and sometimes eventually septicidal (figure 6, 1c), or (3) loculicidal all along the dorsal suture and then often septicidal (figure 6, 2d).

The embryo is straight, 1.5–2.7 mm. long, and embedded in fleshy endosperm. The cotyledons are suborbicular, 0.7–1.7 mm. in diameter, flattened, subcordate at the base and rounded at the apex. Sometimes 2 veins are on each side of the middle of the cotyledon; one pair is basal. The radicle is terete, 0.7–1.1 mm. long, 0.25–0.5 mm. wide, and inferior. A plumule is not evident in the seed stage. Venkata Rao (63) studied the early stages in the development of the embryo of *M. corchorifolia* L.

Cristóbal (6) studied the chromosomes of two species of *Melochia*. In both the diploid number was 18. According to Mangenot & Mangenot (41) the diploid chromosome number of *M. bracteosa* is 14.

Plate 5 illustrates a typical species of *Melochia*. Some floral and fruit characters of a species of each section are illustrated in figure 6.

Taxonomic Position

Melochia is a genus of the family Sterculiaceae sensu lato, tribe Hermannieae.

Schumann (48) included eight tribes in the family. The flowers of the Sterculieae are polygamous, those of the other tribes are hermaphroditic. The petals of the Hermannieae and Helictereae are flat and usually longer than the calyx; those of the Buettnerieae are cucullate at the base and embrace the anthers, often ligulate at the apex, and usually not longer than the calyx. They are absent from the Sterculieae and Fremontieae, absent or minute, glandlike, or squamiform in the Lasiopetaleae, and large in the Dombeyeae. In the Lasiopetaleae the stamens are usually free; they are at least partly united in the other tribes. The staminal tube is greatly elongated in the

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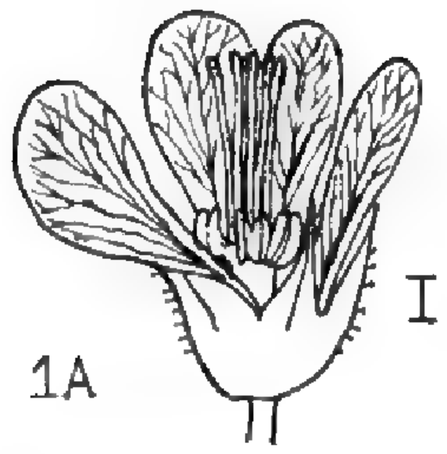
FIGURE 6.—Floral and Fruit Characters of *Melochia*. 1, *Melochia chamaedrys* St.-Hil. var. *chamaedrys*, *Pedersen* 971 (US): A, Flower, one petal removed; B, flower with calyx removed; C, fruit, lateral view; D, fruit, apical view. 2, *Melochia arenosa* Benth., flower, *Dahlgren & Sella* 65 (US); fruit, *Gardner* 2489 (US), syntype: A, Flower, one petal removed; B, flower with parts removed to show essential organs; C, fruit, lateral view; D, fruit, apical view. 3, *Melochia anomala* Griseb., *Venturi* 2108 (US): A, Entire flower; B, flower opened to show essential organs; C, fruit, lateral view; D, fruit, apical view. 4, *Melochia adenodes* A. Goldberg var. *adenodes*, *Hinton* 16203 (US), type: A, Entire flower; B, flower with calyx partly removed; C, D, flower with parts removed to show essential organs; E, fruit, lateral view; F, fruit, apical view. 5, *Melochia umbellata* (Houtt.) Stapf, flower, *Krukoff* 4421 (US); fruit, *Bartlett* 8367 (US): A, Entire flower; B, flower with parts removed to show essential organs; C, fruit, lateral view; D, fruit, apical view. (The scale at the right of each illustration represents 1 mm.)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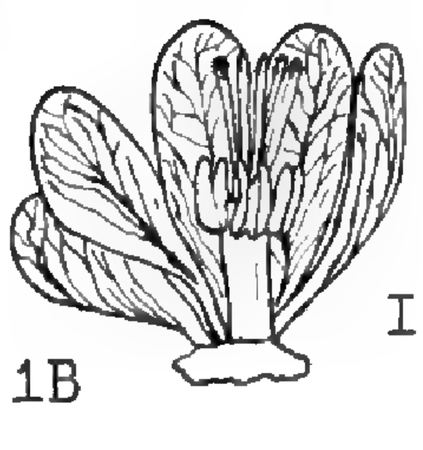
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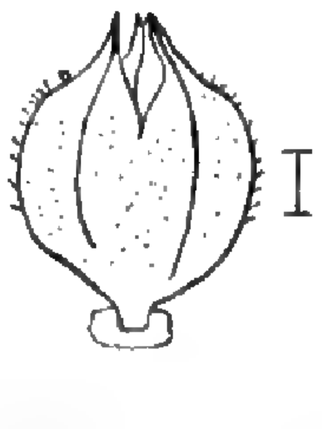
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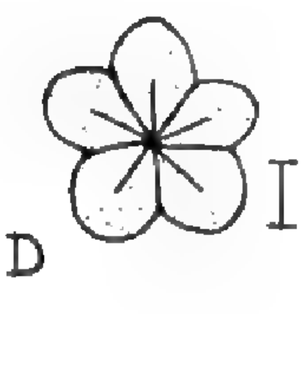
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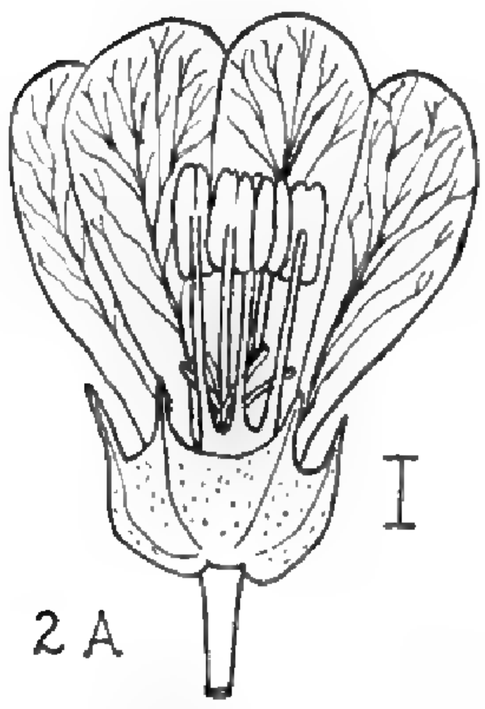
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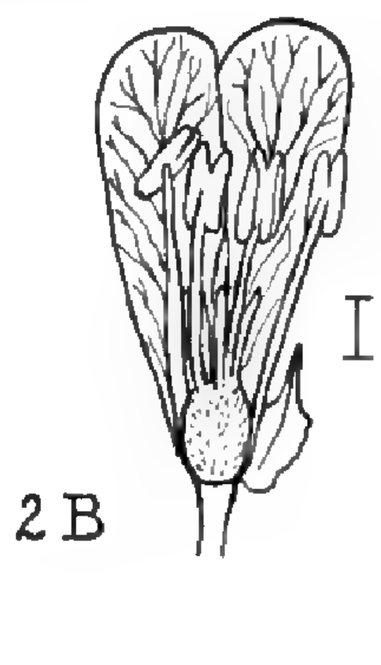
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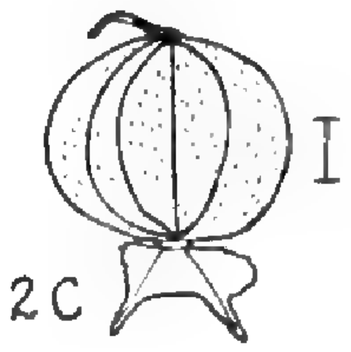
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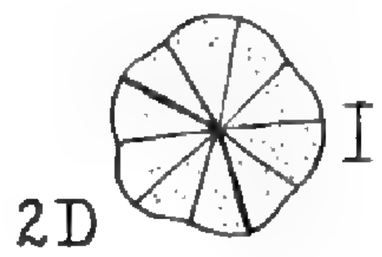
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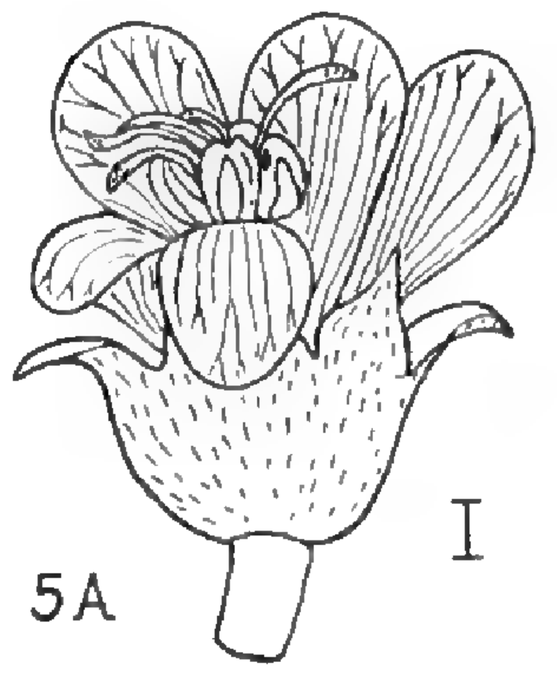
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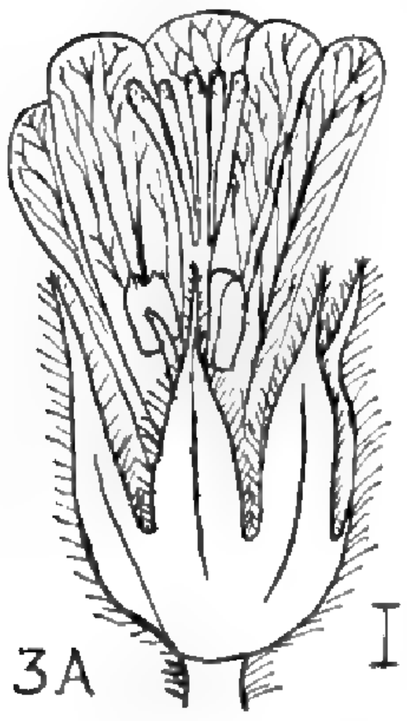
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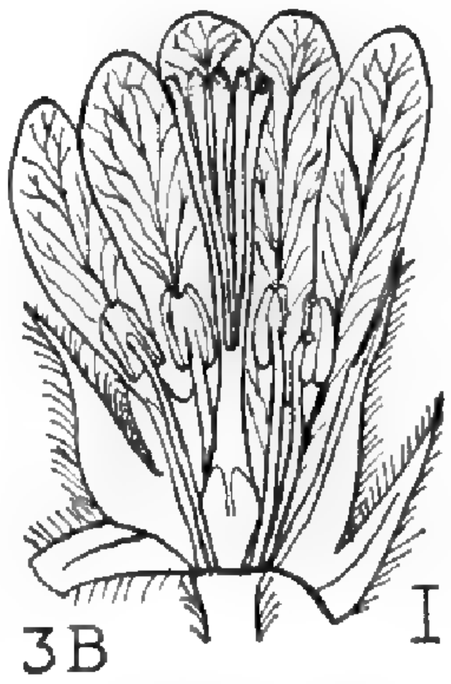
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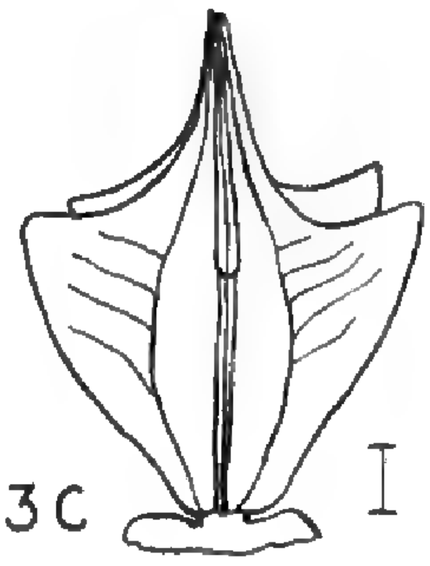
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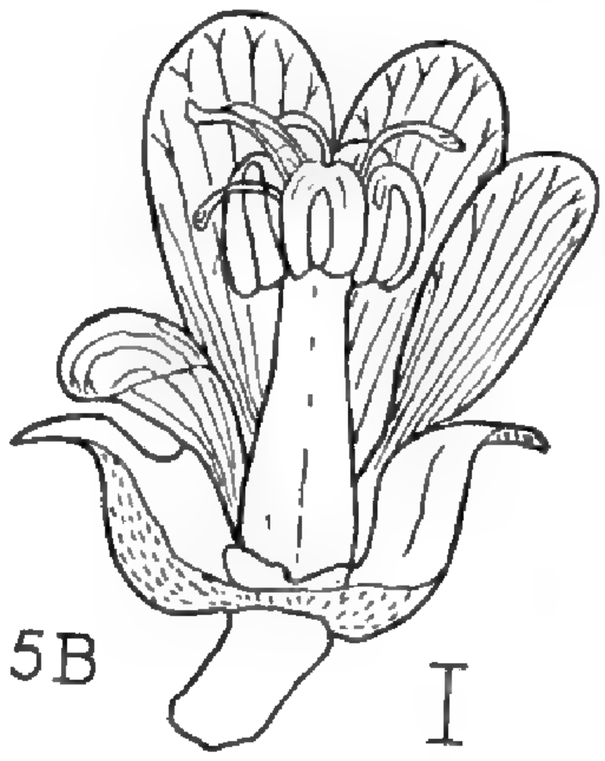
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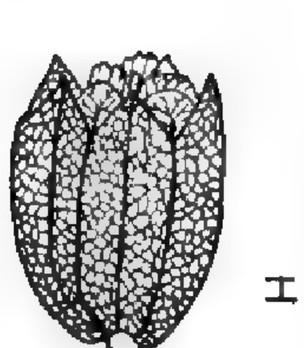
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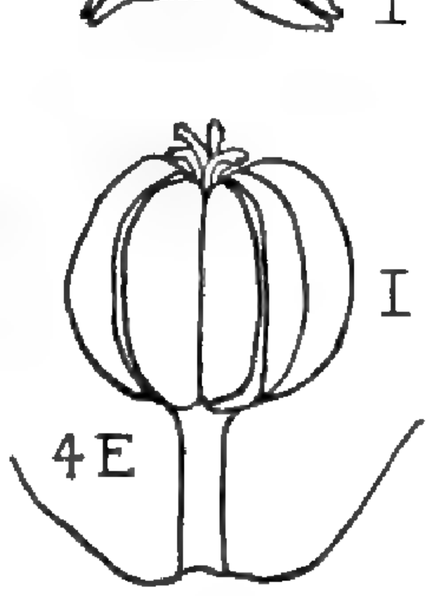
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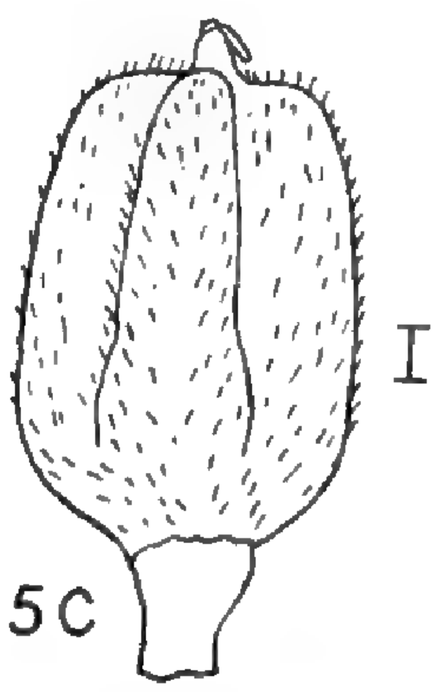
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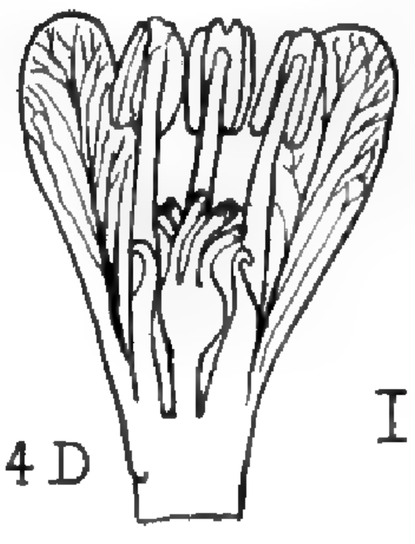
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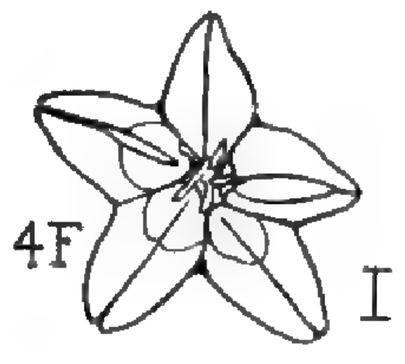
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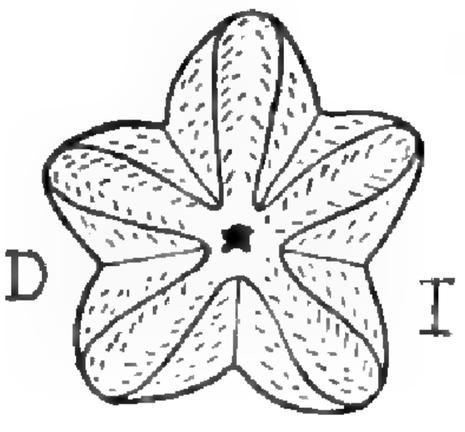
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Eriolaeneae and Fremontieae. The flowers of the Hermannieae have five fertile stamens with dithecous anthers; the stamens of the other tribes are sometimes more numerous and sometimes the anthers are more than dithecous. The gynophore is usually long in the Sterculieae and often so in the Helictereae; it is usually short or absent in the other tribes. The carpels of the Sterculieae are usually separate at anthesis; they are at least partly united in the other tribes.

The tribe Hermannieae contains two subtribes, the Hermanninae and Melochinae. The former contains the genus *Hermannia*. Its pistil consists of five carpels opposite the calyx lobes. Each carpel contains an indefinite number of ovules. The styles are sometimes united at the apex. The seeds are reniform, the embryo is curved, and the cotyledons are oblong and twice as long as wide. The filaments are free or united part way, and the free part is often flattened and broader than the anthers. The anthers are relatively long (about 3 mm. long). The subtribe Melochinae contains *Melochia* and *Waltheria*. The pistil of *Melochia* consists of five antepetalous carpels. Each carpel contains two ovules. The styles are free to the ovary or united part way at the base. The seeds are not reniform, the embryo is straight, and the cotyledons are suborbicular. The filaments are united part way or up to the anthers and the free part is not broader than the anthers. The anthers are shorter (less than 3 mm. long). *Waltheria* differs from *Melochia* primarily in that its pistil consists of one carpel. In *Waltheria* the apex of the style is fimbriate.

Evolution and Relationships

Melochia belongs to a relatively primitive family, the Sterculiaceae, that probably originated at a time when the temperature did not go below freezing, at least not for any considerable period, and moisture was abundantly available in all latitudes. The family migrated from continent to continent. With changes in the climate, it did not survive in colder regions, but at present is well represented in tropical and subtropical areas throughout the world. *Melochia* probably originated in America and the great majority of the species occur here. Members of the genus with primitive characters range from southern Mexico to southern Brazil and northern Argentina, in southeastern Asia, and the Pacific Islands. The three species indigenous to Africa have relatively few primitive characters, and the one species indigenous to Australia is advanced.

Some species flower for extended periods under a variety of conditions; others reproduce only under particular conditions. The former species have a wide distribution.

Species of *Melochia* are usually perennial subshrubs or shrubs, but toward the latitudinal extremes of the range of the genus, and where

available moisture is reduced, the species become herbaceous, and a few are annuals which avoid the rigors of a cold or dry season. Other species have become adapted, by means of a dense indument, to withstand moisture stresses resulting from relatively cool or hot and dry conditions. In species with dense pubescence, stellate hairs are usually more abundant than other types. Stellate hairs occur most commonly in the sections *Pyramis* and *Physodium;* simple ones are most common in the sections *Melochia* and *Mougeotia.* The leaves of species growing in xerophytic habitats are usually thicker than in those that grow under mesophytic conditions. In some species, when the shoot is killed due to unfavorable seasonal conditions, the base of the stem and root remain alive and perpetuate the plant.

As a result of the change to a drier climate, mutant genes tending to enhance survival under xerophytic conditions accumulated. The plants became more compact, and thus conserved moisture by exposing less surface to the environment. For example, leaves became smaller and the internodes of the vegetative stems and inflorescences became shorter. The stipe is well developed in the section *Physodium* but is much reduced or absent in the other sections. The trend was from corymbiform, paniculate, and umbellate inflorescences to spicate, subcapitate, and capitate ones. As is frequently the case in capitate inflorescences, the entire flower or some of its organs become reduced in size. This is especially true of the calyx; in a few species the reduced calyx has become membranous. The sinus between the teeth of the primitive calyx is acute but rounded or truncate in the species with a reduced calyx, and the teeth are short and distant. This trend toward reduction of the calyx is most pronounced in the section *Melochia.* In some species of this section the internodes between the bracts have become reduced so that the latter immediately subtend the flowers; in other species the bracts are enlarged, closely invest the flowers, and take over the protective function of the calyx.

Although some species, such as *Melochia corchorifolia,* have accumulated mutations adapting them to xerophytic conditions, they have retained their ability to grow in mesophytic and hydrophytic habitats.

An evolutionary trend in many lines of organisms is the reduction and loss of parts. In *Melochia* this has occurred in the flower. Staminodes, the vestiges of one of the cycles of stamens, are elongated and most evident in some species of the section *Physodium.* In several species, particularly those of the other sections, they are merely dentiform or entirely absent. The fertile stamens show a trend toward the loss of connective between the anther sacs, so that the species advanced in this respect have deeply emarginate anthers and divergent anther sacs. This is especially the case in the sections *Mou-*

geotia and *Melochia*. The common number of carpels is five, but species primitive with regard to this character frequently have six to eight. There are two ovules in each carpel, but in many species one aborts and only one seed develops.

The primitive colors of the petals appear to be yellow and orange, the most common colors in species of the section *Mougeotia*. In general, plants with rose or purple flowers are more attractive to hymenopterous insects. In a few species of *Melochia* with yellow or orange petals the essential organs are only slightly dimorphic, whereas the heterostylous condition in flowers of different plants of the same species, often associated with insect pollination, is quite evident in rose- and purple-flowered species, predominant in the other sections, except species in which the flowers have become considerably reduced in size.

It is the consensus among botanists that the organs of the flower are homologous with leaves and that, like leaves, in the primitive condition these organs are separate. All species of the genus have partially united sepals; however, the extent of union varies between species. In some species of the section *Melochia* two or three of the bracts may be partially united. In the section *Pyramis* the petals are attached to the staminal tube at the base. In some species of the sections *Mougeotia* and *Melochia* the petals are free of the staminal tube; in others they are attached to it at the base. In these two sections the claw is usually sharply demarcated from the blade of the petal, just as the petiole is demarcated from the blade of the leaf. In the section *Pyramis* the claw is usually not sharply demarcated from the blade of the petal. Ordinarily the petals are free from one another, but in one specimen of a species in the section *Pyramis*, I noticed that the claws were united. In the sections *Melochia* and *Mougeotia* the filaments in the longistylous form of the flower are usually united up to the anthers, but united to a lesser extent in the other sections. In the section *Physodium* the styles are free to the ovary, in the section *Mougeotia* they are usually free to the ovary, and often free in the section *Melochia*, but united at the base in the section *Pyramis*. The cells of the fruit vary in the extent united in the different species. In species of the section *Melochia* the cells are usually united for a greater distance along their sides than in species of the other sections.

The fruits of some species of the section *Mougeotia* dehisce in the most primitive manner, along the ventral suture, the site of union of the infolded carpel phyllomes, and in some species of this section dehiscence is also septicidal. In the section *Visenia* the fruit dehisces ventrally, but it is incompletely septicidal. In other sections dehiscence is first loculicidal along the dorsal suture, the most advanced

means of dehiscence in the genus, and in a few species of the section *Melochia* it is no longer also septicidal.

In *Melochia* the differences between many species are small. I believe that there has been little, if any, extinction of species in the genus. Perhaps the genus has diversified mainly as species became adapted to different climatic conditions and habitats.

Taking into account the above-mentioned evolutionary changes, geographical distribution, and the genetic principle that the similarity of structure among species of the same genus is primarily indicative of genetic relationship, I have arranged the species of *Melochia* according to my understanding of their relationships (fig. 7).

Acknowledgments

I wish to express my appreciation to Dr. Lyman B. Smith, Senior Scientist, United States National Herbarium, for his effort and time expended in my behalf and the patience he has shown in directing my research.

It has been a privilege to use the facilities of the United States National Herbarium for the study of specimens of *Melochia*. I am also grateful to other herbaria in America and Europe and their curators for the loan of specimens. Herbaria are abbreviated according to Lanjouw and Stafleu (34).

The portion of the paper dealing with the American taxa was submitted to the faculty of the Graduate Council of the George Washington University in partial satisfaction of the requirements for the degree of Doctor of Philosophy.

Figure 2 is based on map 19AA, McKinley Publishing Co., Philadelphia, Pa.; all other maps are based on Goode Base Maps, copyright by the University of Chicago Press.

Systematic Treatment

Melochia L.

Melochia L. Sp. Pl. I. 2:674. 1753.
Visenia Houtt. Handleid. 8:308. 1777.
Moluchia Medic. Malv. 10. 1787.
Meluchia Medic. *in* Staatsw. Vorles. Churpf. Phys. Oek. Ges. 1:217. 1791.
Riedlea Vent. Choix. 37, pl. 37. 1803.
Altheria Thou. Gen. Nov. Madagascar. 19. 1806.
Mougeotia H. B. K. Nov. Gen. & Sp. 5:326, pl. 483, 484. 1823.
Riedleia DC. Prodr. 1:490. 1824.
Aleurodendron Reinw. *in* Sylloge Ratisbonn 2:12. 1828.
Glossospermum Wall. Cat. n. 1153. 1829.
Riedlia Dumort. Anal. Famil. 46. 1829.
Polychlaena G. Don, Gen. Syst. 1:488. 1831.

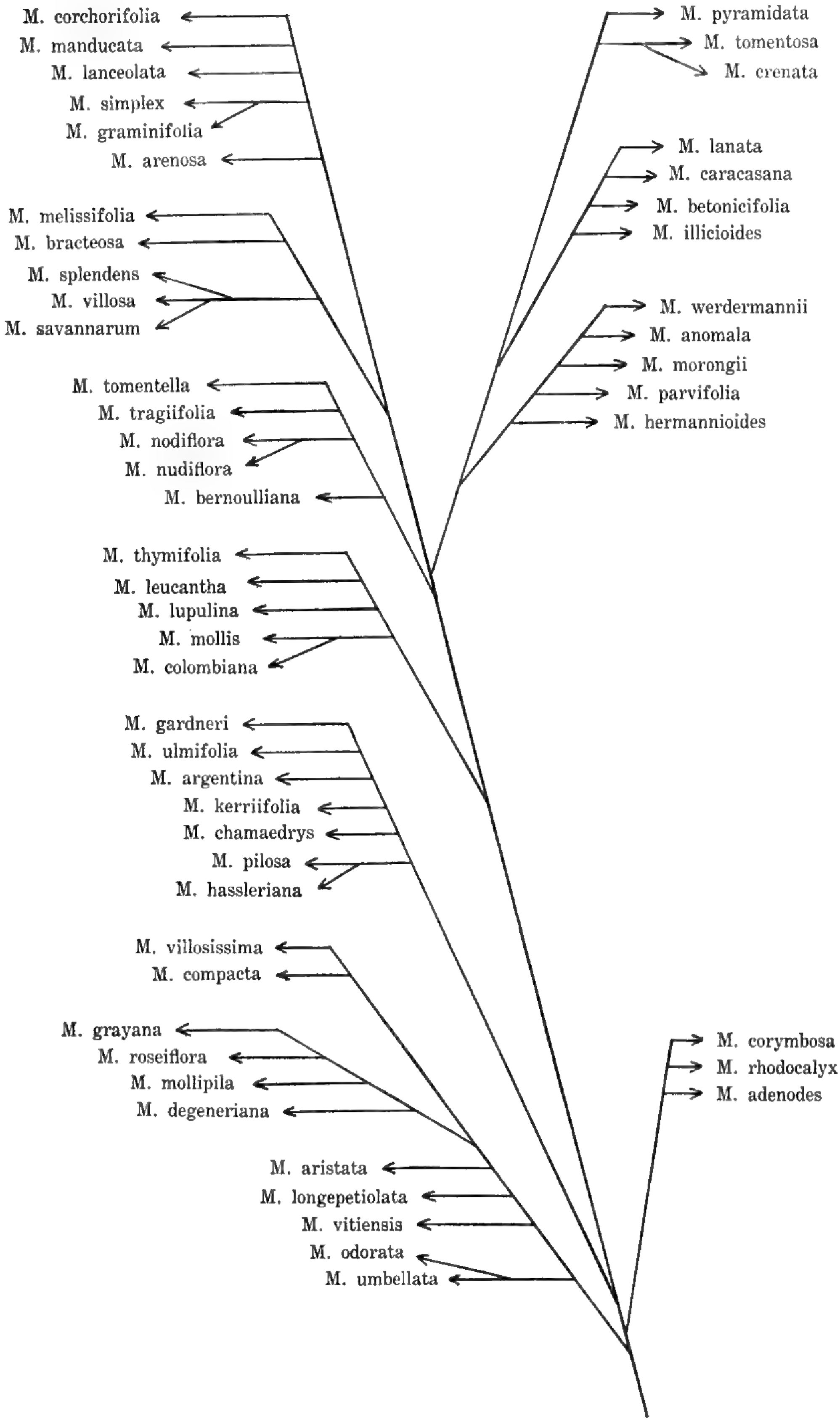

FIGURE 7.—Relationships of the species of *Melochia*.

Physodium Presl, Rel. Haenk. 2:150. 1836.
Lochemia Arn. *in* Ann. Sc. Nat. 2 sér. 11:172. 1839.
Ridleia Endl. Gen. 1000. 1840, attributed to Vent.
Riedleja Hassk. Catal. Pl. Hort. Bog. Alt. 205. 1844.
Anamorpha Triana & Karst. *in* Triana, Nuev. Jen. i Esp. Fl. Neo-Granad. 9. 1854.
Physocodon Turcz. Bull. Nat. Mosc. 31(1):212. 1858.

Mostly shrubs or subshrubs, sometimes herbs or small trees, 0.08–15.0 (–20) meters high, mostly perennial, often with a woody taproot, sometimes 2–5 times thicker than the base of the stem and 0.4–2.2 cm. wide, the young stems subglabrous to cinereous or canescent, hirsute, pilose, sericeous, or tomentulose, hairs stellate, simple, forked or glandular, sometimes tan, golden, or ferruginous, 0.05–4.0 mm. long, the internodes 0.2–18.5 cm. long; leaves simple, alternate; stipules 1.5–10.3 mm. long, 0.2–4.0 (–12) mm. wide, deltoid-acuminate or deltoid-acute, generally lanceolate or linear, sometimes ovate or suborbicular, usually ciliate and hirsute, tomentulose or sericeous, hairs simple, stellate, forked or glandular, 0.05–3.5 mm. long; petiole 0.07–14.5 (–20.5) cm. long; lamina 0.6–24 (–30) cm. long, 0.2–21.5 (–27) cm. wide, ovate, lanceolate, linear, oblong-ovate, suborbicular, or elliptic, one side sometimes larger than the other, the base usually rounded to cordate, sometimes truncate, cuneate or oblique, the apex usually acute to acuminate, sometimes rounded, both surfaces glabrous, hirsute, sericeous or tomentulose and canescent or cinereous or brownish, sometimes velutinous or lanate, hairs stellate, simple, forked, or a combination of these, sometimes also glandular, 0.05–4.0 mm. long, rarely covered with resin-colored granules or pulverulent, the margin usually irregularly crenate-serrate, serrations 0.3–12.0 mm. wide, 0.2–3.6 mm. high, 4–15 pairs of primary veins, usually 2 being basal, usually impressed above and prominent beneath.

Inflorescences axillary, terminal, leaf-opposed, or 90° from the leaf, umbellate, subcapitate, paniculate, spicate or corymbiform, cymose, 0.6–34 cm. long, the peduncle 0–11 (–16) cm. long, sometimes with a primary branch 0.2–5.2 (–7.0) cm. long, a secondary one up to 2.0 (–4.0) cm. long, a tertiary one up to 1.6 (–3.0) cm. long, and rarely a quaternary one up to 2 cm. long, the pedicel 0–14 (–19) mm. long; bracts 0.5–12.2 mm. long, 0.1–3.9 (–14) mm. wide, sometimes 2–3 immediately subtending each flower, at other times at the base of the pedicel, sometimes 2–3 united part way; flowers: few to numerous, fertile stamens 5, antepetalous, staminodes usually absent, sometimes 5, alternate with the stamens, 0.1–1.2 mm. long, usually dentiform, sometimes elongated, the anthers 0.4–2.6 mm. long, 0.3–1.4 mm. wide, oblong, emarginate at both ends, sometimes nearly to the middle from the apex, the carpels 5, rarely 6–8, antepetalous, styles filiform, sometimes slightly clavate at the apex, ovules 2 per carpel.

Calyx quinquefid, valvate in aestivation, persistent, usually green, sometimes rose, rose purple, yellow, orange, red, or pinkish brown, sometimes canescent, sometimes membranous, 1.4–15.0 mm. long, 2.1–10 mm. wide, the teeth 0.4–7.8 mm. long and 0.2–4.8 (–5.5) mm. wide, sometimes accrescent, becoming up to 36 mm. long and 19 mm. wide, with teeth up to 12 mm. long and 10 mm. wide, the teeth usually deltoid-acute or deltoid-acuminate, sometimes ovate or nearly linear, hirsute, tomentulose, or sericeous, sometimes ciliate, hairs simple, stellate, glandular, or forked, 0.05–2.3 (–4.0) mm. long, the sinus usually acute, sometimes rounded to truncate; petals purple, pink, purple distally and yellow or orange proximally, yellow, orange, white, blue, red, white with red stripes, or violet, 2.7–17.4 mm. long, 0.8–9.5 mm. wide, usually obovate or oblanceolate, sometimes obdeltoid, obovate-oblong, elliptic, oval, ovate or oblong, cuneate or spatulate, free of the staminal tube or attached to it for 0.3–5.0 mm., the claw 0–6.5 mm. long, rarely glandular tissue present between the calyx and corolla, with lobes extending between the bases of the petals, sometimes a few glandular, simple, forked, or stellate hairs on the petals.

Longistylous form. Stamens 2.4–7.0 (–9.0) mm. long, the filaments united up to the anthers or free for 0.2–3.0 mm., sometimes a few hairs at the base of the staminal tube; pistil 2.6–10.9 (–12) mm. long, the styles free for 1.2–6.7 mm., to the ovary or united for 0.3–4.0 mm., papillose at the apex for 0.5–2.5 mm.

Brevistylous form. Stamens 2.8–11.3 mm. long, sometimes with a few hairs at the base of the staminal tube, the filaments free for 0.5–7.5 mm.; pistil 2.3–6.9 (–8.0) mm. long, the styles free for 0.8–5.3 mm., to the ovary or united for 0.2–3.0 mm., papillose for 0.3–1.0 mm. at the apex.

The flowers of several species in the section *Melochia* not dimorphic, stamens and pistils 1.7–3.2 mm. long, the filaments free for 0–1.2 mm., the styles free for 0.6–1.2 mm., to the ovary or united for 0.1–0.3 mm.

Fruit schizocarp or capsule, 2.4–10.5 (–12) mm. long, 2.9–17.0 (–22) mm. wide, subglobular and pentagonal, pyramidal and pentapterous, ovoid or oblong, the sulci between the carpels shallow to deep, extending a fifth to half way to the center of the fruit, usually hirsute, tomentulose, or sericeous, subglabrous to canescent, hairs stellate or simple, sometimes also forked or glandular, 0.1–1.6 mm. long, the stipe 0–6.7 mm. long; dehiscence septicidal, loculicidal, or both; seeds brown to black, 1 or 2 per cell, 1.4–3.9 mm. long, 0.9–2.5 mm. wide, usually trigonal, the dorsal surface rounded and the sides flat, sometimes obovate, sometimes somewhat flattened, in one section the seed may have an ascending membranous wing 0.3–5.3 mm. high and 0.7–3.0 mm. wide.

The flowering and fruiting periods are usually long, sometimes throughout the year.

TYPE SPECIES: In the current International Code of Botanical Nomenclature (33), it is agreed to associate generic names which appear in Linnaeus' Species Plantarum, edition 1, 1753, with the first subsequent description given under those names in Linnaeus' Genera Plantarum. In edition 5, 1754, of the latter, Linnaeus cited Dillenius (9) under *Melochia*, and the latter only described *Melochia corchorifolia* in *Melochia*. I therefore consider *Melochia corchorifolia* L. to be the type species of the genus. The proposal of *M. pyramidata* L. as lectotype by Hitchcock and Green (International Botanical Congress, 1930) has no official standing.

DISTRIBUTION: In tropical and subtropical regions, from southern United States to northern Argentina and Uruguay, and the West Indies, India and southeast Asia, Indonesia, the Philippines, and other Pacific Islands to the Tuamotu Islands, in savanna, thickets, fields, or forests, sometimes on hillsides, usually in sun, in dry or wet habitats, on various types of soil, at 0–3,150 meters elevation.

Key to Sections of *Melochia*

1. Fruit slightly retuse at the apex, stipe 4.3–6.7 mm. long; calyx accrescent, becoming 15–36 mm. long; staminodes often present, up to 1.2 mm. long. Section V. **Physodium**

1. Fruit not retuse at the apex, stipe 0–1.5 mm. long; calyx not accrescent or, if accrescent, not exceeding 13 mm. in length; staminodes rarely present, to 0.4 mm. long.

2. Fruit pyramidal (ovoid in *M. crenata*), pteratus, loculicidally dehiscent along the entire dorsal sutures (*M. hermannioides* tardily dehiscent), sometimes also dehiscent along the ventral sutures and septicidal; inflorescences usually leaf-opposed . . . . . Section IV. **Pyramis**

2. Fruit subglobular or ovoid, sometimes acute at the apex, apterous but dorsum of carpels sometimes keeled, dehiscence various; inflorescences axillary, terminal or both (sometimes also leaf-opposed in *M. degeneriana*).

3. Fruit first loculicidally dehiscent all along the dorsal suture, usually later septicidal; sinus between calyx teeth usually rounded to truncate, rarely acute, teeth often distant; dorsum of carpels of fruit rounded. Section III. **Melochia**

3. Fruit (1) septicidally dehiscent into cocci with a narrow ventral slit or (2) loculicidal all along the ventral suture, the cells gaping ventrally, and usually also 0.2–0.5 the way along the dorsal suture, sometimes eventually septicidal; sinus between calyx teeth usually acute, sometimes narrowly rounded; dorsum of carpels of fruit often somewhat keeled, especially at the distal end.

4. Fruit often falling apart, the dehiscence often completely septicidal, carpels usually 5, rarely 6, seeds wingless; peduncle sometimes absent, usually without branches from it; herbs or shrubs, rarely a tree to 5 meters high . . . . . Section II. **Mougeotia**

4. Fruit persistent, the dehiscence incompletely septicidal, carpels often 6–8, seeds often winged, the wing 0.3–5.3 mm. high, 0.7–3.0 mm. wide; peduncle always present, usually branches from it; shrubs or trees to 15 (–20) meters high . . . . . Section I. **Visenia**

Key to Species of *Melochia*

SECTION I. VISENIA

1. Fruit suboblong, intercarpellary sulci extending the entire length of the fruit, dehiscence usually only along the ventral sutures; stipules generally broad (5–12 mm. wide), usually suborbicular, the apex rounded; seed wing large (4–5.3 x 2–3 mm.) . . . . . **1. M. umbellata**
1. Fruit ovoid, intercarpellary sulci usually only marked in distal half of the fruit, dehiscence partly along the dorsal sutures as well as along the ventral sutures; stipules narrower (usually less than 4 mm. wide), deltoid, lanceolate or ovate, the apex acute or acuminate; seed wingless or wing smaller (0.3–3.5 x 0.7–2.2 mm.).
2. Leaves lanceolate or elliptic, narrow, 1.1–2.4 (–4.5) cm. wide, subcoriaceous; shrub 1.5–2 meters high. . . . . **9. M. grayana**
2. Leaves mostly or all ovate, at least some 5 or more cm. wide; plant often more than 2 meters high.
3. Leaves persistently canescent, woolly on both surfaces, hairs to 1.2 mm. long; young stems densely hairy, hairs to 2.0 mm. long; flowers in rather compact cluster (i.e., pedicels short) . . . . . **11. M. villosissima**
3. Leaves glabrescent, hairs usually 0.5 mm. long or shorter (1 mm. long in *M. compacta*); hairs on young stems 0.6 mm. long or shorter.
4. Seeds wingless or if wing present less than 1 mm. long and wide.
5. Inflorescences usually compact, primarily due to short pedicels (mostly 0–2 mm. long); bracts relatively broad (0.8–3.0 mm. wide); internodes short (0.5–1.0 cm. long); indument relatively long (to 1.0 mm.); in longistylous form of the flower the filaments united up to the anthers or free for 0.5 mm. . . . . **10. M. compacta**
5. Inflorescences fairly loose, the pedicels to 7 mm. long in fruiting stage; bracts narrower (0.5–1.7 mm. wide); internodes usually longer; indument shorter (to 0.5 mm.); in longistylous form of the flower the filaments free for 1.2–1.5 mm.
6. Calyx 5.8–8.6 mm. long; fruit 4–6 (–8) mm. long, sometimes without an arista; bracts 3.7–5.5 mm. long; leaf serrations to 2.4 mm. high; internodes 0.3–3.0 cm. long; seed not aristate. **2. M. odorata**
6. Calyx 4.0–5.5 mm. long; fruit 6.2–10.5 mm. long, aristate; bracts 2 mm. long; leaf serrations to 1.5 mm. high; internodes 0.7–8.3 cm. long; seed sometimes aristate . . . . . **5. M. aristata**
4. Seeds winged, at least some wings 1 mm. or more long and wide (0.6–3.5 x 0.7–2.2 mm.).
7. Inflorescences long (17.5–21.5 cm.); petioles long (2–19 cm.); petals salmon pink . . . . . **4. M. longepetiolata**
7. Inflorescences shorter (3–14 cm.); petioles shorter (0.3–9.5 cm.); petals usually bright pink, yellow or white.
8. Petioles short (0.3–1.5 cm.) . . . . . **8. M. roseiflora**
8. Petioles generally longer (0.3–9.5 cm.).
9. Serrations of leaves up to 2.5 mm. high.

10. Fruit 4–6 mm. long, 4–6.5 (–8.0) mm. wide; calyx 5.8–8.6 mm. long, 6.1–8.0 mm. wide; petals usually pink.
2. M. odorata

10. Fruit larger, 7–9 mm. long, 7.0–7.5 mm. wide; calyx generally smaller 3.5–6.0 mm. long, 3.8–6.7 mm. wide; petals yellow or white . . . . . **3. M. vitiensis**

9. Serrations of leaves up to 1.1 mm. high.
11. Fruit 9–10 mm. long, 6–7.2 mm. wide; lower surface of leaf subglabrous . . . . . **6. M. degeneriana**

11. Fruit smaller, relatively broader, 5–7.5 mm. long, 5.3–9.4 mm. wide; lower surface of leaf tomentulose.
7. M. mollipila

SECTION II. MOUGEOTIA

1. Primary dehiscence septicidal into cocci with a narrow slit along the ventral suture, sometimes also for 0.33–0.5 the way along the dorsal suture, or readily split for 0.25–0.5 the way along the dorsal suture.

2. Calyx considerably accrescent, becoming 7–12.3 mm. long, 7.7–12 mm. wide.
3. Calyx becoming 8–12.3 mm. long, and up to 12 mm. wide; peduncle slender and short, typically 0.3–0.5 mm. wide, and 0.1–0.7 cm. long, often 2 or 3 per leaf axil; hairs not brownish, predominantly simple on the upper surface of the lamina . . . . . **22. M. lupulina**

3. Calyx becoming 7–9.5 mm. long, 7.7–10 mm. wide; peduncle relatively thick and long, typically 0.5–1.5 mm. wide and 0.5–8.0 cm. long, usually 1 per leaf axil; hairs often brownish, stellate hairs predominant, or as common as the simple ones, on the upper surface of the lamina; lamina and stems more densely hairy than those of *M. lupulina*.
19. M. mollis

2. Calyx not accrescent or only slightly so, 3.1–7.0 mm. long, 3–6.5 mm. wide.
4. Inflorescences slender, open, somewhat paniculate; peduncles very slender, 0–2.0 cm. long; pedicels slender and long, 3–7 mm. long; serrations of lamina large, up to 3.5 mm. high; lamina not canescent or cinereous, hairs simple and stellate on the upper surface . . . **24. M. bernoulliana**

4. Inflorescences usually glomerate or corymbiform; peduncles sometimes absent; pedicels shorter, typically 1–3 mm. long; serrations of lamina shorter.
5. Inflorescences usually corymbiform, sometimes paniculate; young stems and leaves canescent-cinereous, hairs stellate, 0.1–0.3 mm. long.
21. M. leucantha

5. Inflorescences neither corymbiform nor paniculate; young stems and leaves usually not canescent-cinereous, simple and longer hairs usually also present.
6. Internodes short, 0.4–0.7 cm. long; petioles short, 0.2–0.5 cm. long; peduncles 1.2–1.6 cm. long, branched . . . . . **20. M. colombiana**

6. Internodes and petioles usually longer than 1 cm.; peduncles often absent.
7. Peduncles relatively thick, 0.5–1.5 mm. wide, and usually relatively long, 0.5–8.0 cm. long, sometimes branched.
19. M. mollis

7. Peduncles slender, usually shorter and not branched, often absent.
8. Young stems predominantly covered with glandular hairs; simple hairs on the upper surface of the lamina more or less erect; peduncle absent . . . . . **27. M. tragiifolia**

8. Young stems without glandular hairs or with very few; simple hairs on the upper surface of the leaf appressed.
9. Peduncle 0–4.0 cm. long; pedicels 0.5–3 (–4) mm. long; bracts narrow, 0.2–1.1 mm. wide . . . . **23. M. thymifolia**
9. Peduncle 0–1.0 cm. long; pedicels usually shorter, 0–2 (–3) mm. long, bracts narrow or wide.
10. Leaves predominantly lanceolate and acuminate, up to 3.9 cm. wide . . . . . **28. M. tomentella**
10. Leaves predominantly ovate, usually acute, up to 7.7 cm. wide.
11. Bracts mostly broad, 0.6–3.9 mm. wide; lower surface of leaf tomentulose; inflorescences commonly terminal as well as axillary . . . . . **26. M. nudiflora**
11. Bracts narrow, 0.2–1.1 mm. wide; lower surface of leaf usually subglabrous; inflorescences glomerate, usually of numerous flowers, at up to 20 axillary nodes, usually not terminal too . . . . . **25. M. nodiflora**

1. Primary dehiscence of the fruit loculicidal along the ventral suture, so that the cells are gaping ventrally, and 0.2–0.5 the way along the dorsal suture, sometimes also finally septicidal.
12. Inflorescences corymbiform, open, fairly large, 6 cm. long, 5 cm. wide, axillary; lamina large, 5–14 cm. long, 2–8.2 cm. wide; a tuft of hairs 0.1–0.2 mm. long at base of petal blade; calyx and corolla short (4.3–6.1 mm. long) . . . . . **17. M. ulmifolia**
12. Inflorescences not corymbiform, sometimes contracted, often smaller, terminal, axillary, or both; lamina usually smaller, 0.8–9.5 (–12) cm. long, 0.2–7.5 cm. wide; no hairs at base of petal blade.
13. Inflorescence a dense terminal spike, sometimes also axillary, 4–5 cm. long; calyx (7–8.3 mm.), petals (11.6–12 mm.), pistil in longistylous form (11–12 mm.) and fruit (7 mm.) relatively long. **18. M. gardneri**
13. Inflorescences axillary, or axillary and terminal, usually paniculate, racemose, or umbellate; calyx, petals, pistil in longistylous form and fruit often shorter.
14. Fruit large, 6.7–7.5 mm. long, 4.5–6.5 mm. wide; serrations of leaves large, 0.7–3.6 mm. high; leaves subglabrous; stamens and pistils subequal (4.8–5.6 and 4.2–5.1 mm., respectively). **16. M. argentina**
14. Fruit smaller, 3.7–6.0 mm. long, (3–)3. 5–5.6 mm. wide; serrations of leaves smaller, 0.3–2.7 mm. high; leaves sometimes quite hairy.
15. Inflorescences primarily or entirely axillary; lamina small, 1–4.3 (–6.5) cm. long, 0.8–3 (–4.5) cm. wide, usually broadly ovate or suborbicular; plant procumbent or ascending, small, 0.1–0.5 meter long . . . . . **14. M. chamaedrys**
15. Inflorescences primarily terminal; lamina usually larger, usually ovate or lanceolate; plant often erect and larger.
16. Fruits usually in pairs; leaves subglabrous; calyx short, 3–4.7 mm. long . . . . . **15. M. kerriifolia**
16. Fruits not in pairs; leaves usually sericeous-pilose; calyx usually longer, (4–) 4.6–7.8 mm. long.
17. Lamina long-ciliate, hairs on surfaces also long, 1.3–4.0 mm. long; peduncles 0.5–3.0 cm. long; pedicels 2.5–4.0 (–6) mm.

long; flowers evenly distributed about the inflorescence branchlets; inflorescences up to 6.5 cm. long. **13. M. hassleriana**

17. Lamina not ciliate, hairs on surfaces up to 1.3 mm. long; peduncles and pedicels usually shorter; flowers sometimes more frequent on the upper side of the inflorescence branchlets; inflorescences to 20 (–31) cm. long and usually flowers more numerous . . . . . **12. M. pilosa**

SECTION III. MELOCHIA

1. Leaves linear, at least 10 times longer than wide, entire or obscurely serrate, glabrous or subglabrous . . . . . **36. M. graminifolia**
1. Leaves not linear, less than 10 times longer than wide, serrations evident.
   2. Leaves densely tomentulose, at least the lower surface canescent, all or almost all hairs very short (0.1 mm.), stellate, the rays numerous (8–12 per hair); inflorescences axillary, pedunculate, umbellate . **34. M. arenosa**
   2. Leaves not tomentulose-canescent, or if so, inflorescences primarily terminal or if axillary, not pedunculate.
      3. Flowers not dimorphic, androecium and gynoecium equal in length; calyx short, 1.5–2.6 mm. long.
         4. Inflorescences principally or entirely terminal.
            5. Inflorescences subcapitate, leaves mostly ovate . **39. M. corchorifolia**
            5. Inflorescences corymbiform, leaves lanceolate . . **38. M. lanceolata**
         4. Inflorescences principally or entirely axillary.
            6. Fruit small, 2.4–2.5 mm. long, 3.2–3.3 mm. wide, with simple hairs; inflorescences not pedunculate; lamina small, 0.7–3.5 cm. long, 0.6–1.6 cm. wide . . . . . **33. M. melissifolia**
            6. Fruit larger, 2.7–4.0 mm. long, 3.8–4.8 mm. wide, with glandular and simple hairs; inflorescences often pedunculate; lamina larger, 3–7.5 cm. long, 0.9–6.2 cm. wide . . . . . **37. M. manducata**
      3. Flowers dimorphic on different plants, androecium and gynoecium differing in length; calyx usually longer, 2.4–6.0 mm. long.
         7. Leaves lanceolate to suboblong, nearly linear near the apex of the stem, a few scattered hairs on the upper surface; staminal tube glabrous; peduncles 0.2–4.1 cm. long . . . . . **35. M. simplex**
         7. Leaves usually ovate, if primarily lanceolate, then densely tomentulose; staminal tube usually puberulous; peduncles 0–0.1 cm. (rarely to 3.0 cm.) long.
            8. Plants small, usually prostrate, 0.2–0.6 meter long; lamina small, 1–2.2 cm. long, apex usually rounded (Isle of Pines and Pinar del Rio, Cuba) . . . . . **30. M. savannarum**
            8. Plants usually larger, more erect; lamina usually larger, 1.5–10.5 cm. long, apex usually acute.
               9. Inflorescences primarily terminal . . . . . **29. M. villosa**
               9. Inflorescences primarily axillary.
                  10. Petiole short, 0.1–0.4 cm. long, base of lamina cuneate to rounded, serrations short, 0.2–0.8 mm. high; pedicels absent or very short, to 1 mm. long; calyx 5–5.2 mm. long; petals narrow, 1.7–2.0 mm. wide . . . . . **31. M. splendens**
                  10. Petiole longer, to 2.3 cm. long, base of lamina rounded to subcordate, serrations higher, to 2.0 mm. high; pedicels present, longer, to 3.5 mm. long; calyx shorter, less than 5 mm. long; petals wider, to 3.5 mm. wide . . . . . **32. M. bracteosa**

SECTION IV. PYRAMIS

1. Upper surface of leaves densely sericeous-tomentose, yellow-tan-canescent, and lanate, hairs simple, appressed, 0.5–2.0 mm. long, lower surface densely tomentose, yellow-tan-canescent, hairs stellate, forked and simple, 0.7–1.6 mm. long; peduncles relatively thick, 1.2 mm. wide . . . **48. M. lanata**

1. Upper surface of leaves not densely sericeous-tomentose, nor yellow-tan-canescent and lanate, hairs shorter and other types often also present, lower surface often not densely tomentose, hairs shorter; peduncles thick or slender.
   2. Fruit large, 10–12 mm. long, 19–22 mm. wide, chartaceous, truncate or very shortly rostrate (1 mm.) at the apex, alae relatively broad, and blunt at the lateral angle . . . . . **45. M. illicioides**
   2. Fruit smaller, 5–10.5 mm. long, 3.8–17 mm. wide, somewhat indurate, apex usually acute, rostrum short or long, alae usually narrower, and acute, acuminate or rounded at the lateral angle.
      3. Fruit ovoid, pentapterous, 10–10.5 mm. long, 6.7–8.7 mm. wide, the lateral angle of the alae obscure; pedicels long, 4–7 mm. long; lamina oval to broadly ovate, the apex rounded . . . . . **50. M. crenata**
      3. Fruit pyramidal, pentapterous, often smaller, the lateral angle of the alae evident; pedicels often shorter; lamina usually ovate or lanceolate, the apex often acute.
         4. Fruit narrow, both absolutely and relative to length, 6–7 mm. long, 3.8–4.8 mm. wide; entire plant canescent, tomentulose, hairs stellate, 0.3–1.0 mm. long; peduncles short and relatively thick, 0.2–0.8 cm. long, 1.2–1.5 mm. wide; pedicels short, 1.5–2.0 mm. long. **44. M. werdermannii**
         4. Fruit usually broader, 4–14 mm. wide; plant often neither canescent nor tomentulose, hairs sometimes simple, forked or glandular as well as stellate; peduncles sometimes longer and slender; pedicels sometimes longer, to 6 mm. long.
            5. Plants prostrate, small, 0.1–0.5 meter long; lamina small, 0.9–2.1 cm. long, 0.6–1.4 cm. wide, usually rounded at both ends, sometimes cuneate at the base, crenations relatively large, 0.5–1.9 mm. high, not extending to the base of the lamina; fruit tardily dehiscent, lateral angle of the alae above the middle of the fruit. **40. M. hermannioides**
            5. Plants usually erect, rarely decumbent, often larger; lamina usually larger, often acute at the apex, crenations or serrations relatively smaller, usually extending to the base of the lamina; fruit readily dehiscent, lateral angle of the alae usually at, or below, the middle of the fruit.
               6. Lamina usually obovate or elliptic, rarely ovate, the base cuneate or rounded, the apex rounded, relatively small, 0.6–4.5 cm. long, 0.3–2.8 cm. wide; petiole short, 0.1–1.2 cm. long; flowers usually white . . . . . **41. M. parvifolia**
               6. Lamina usually ovate or lanceolate, the base not cuneate, the apex often acute, usually larger; petiole usually longer; flowers often colored.
                  7. Fruit relatively short and narrow, 6–7 mm. long, 4–5.8 mm. wide; peduncle often relatively long, up to 4 cm. long; calyx relatively long, 6.7–10.2 mm. long . . . . . **42. M. morongii**
                  7. Fruit often longer and broader, typically 7–8.5 (–10.5) mm. long

and 6.6–11 (–17) mm. wide; peduncle often shorter, typically to 2.5 cm. long; calyx usually shorter, typically 5–8.5 mm. long.

8. Peduncle short, typically 0–0.5 cm. long; pedicels short, 1–2 mm. long; fruit relatively narrow, (5.5–) 6.2–7.0 mm. wide; serrations of lamina fairly large, to 2.5 mm. high, hairs of lamina to 1.2 mm. long . . . . . **43. M. anomala**

8. Peduncle usually longer, typically 1–2 cm. long; pedicels usually 1–4 mm. long; fruit wider, typically 8 (–17) mm. wide; serrations of lamina usually smaller, hairs of lamina often shorter.

9. Peduncles slender, 0.4–0.6 mm. wide; inflorescences umbellate, typically 2–10 flowers per inflorescence; flowers usually purple, pink, violet, blue, or purple distally and yellow proximally.

10. Inflorescences mostly leaf-opposed; leaves usually sparsely pubescent, hairs simple, forked, stellate and sometimes also glandular; fruit often purple-blotched, rostrum 0–2.1 mm. long, point of alae acute or acuminate; plant 0.08–2.0 meters high; calyx 3.7–6.2 mm. long . . . . . **51. M. pyramidata**

10. Inflorescences mostly axillary; leaves often densely tomentose and canescent, hairs stellate; fruit not purple-blotched, rostrum 1.3–5.0 mm. long, point of alae acute or rounded; plant 0.3–4.0 meters high; calyx 5–8.6 mm. long . . . . . **49. M. tomentosa**

9. Peduncles relatively thick, 0.8–1.4 mm. wide; inflorescences subcapitate, typically 3–20 flowers per inflorescence; flowers usually white or yellow, rarely purple.

11. Peduncle usually axillary, 0.8–2.9 cm. long; fruit 11.5–17 mm. wide; lower surface of lamina sometimes canescent (Brazil) . . . . . **46. M. betonicifolia**

11. Peduncle often leaf-opposed, 0.4–2.0 cm. long; fruit 6–11 mm. wide; lamina generally more densely pubescent and hairs often yellowish (mostly Venezuela and Colombia) . . . . . **47. M. caracasana**

SECTION V. PHYSODIUM

1. Petals 16–17.4 mm. long, 5.6–9.5 mm. wide, markedly exceeding the calyx in length at anthesis; hairs of calyx stellate, 0.2–0.5 mm. long; staminodes none or rarely 0.1 mm. long . . . . . **53. M. rhodocalyx**

1. Petals 8–12 mm. long, 2–2.7 mm. wide, not exceeding or slightly exceeding the calyx in length at anthesis; hairs of calyx stellate or glandular; staminodes none or to 1.2 mm. long.

2. Calyx and pedicels covered with glandular hairs 0.2–0.6 mm. long and a few stellate hairs 0.1–0.2 mm. long; petals 8–12 mm. long, 2–2.7 mm. wide, not exceeding the calyx in length at anthesis; staminodes 0.2–1.2 mm. long . . . . . **52. M. adenodes**

2. Calyx and pedicels covered with stellate hairs 0.1–0.8 mm. long; petals 9.7 mm. long, 2.1 mm. wide, slightly exceeding the calyx at anthesis; staminodes none . . . . . **54. M. corymbosa**

Section I. *Visenia* K. Schum. *in* Engler & Prantl, Pflzfam. III 6: 81. 1890

Shrubs or small trees 0.7–15 (–20) meters high, the young stems and petioles tomentulose or tomentose, hairs fuscous or cinerescent, stellate, and often also forked and simple, 0.05–2.0 mm. long, the internodes 0.2–18.5 cm. long; stipules often soon deciduous, 2–10 mm. long, 0.5–12 mm. wide, deltoid-acute or deltoid-acuminate, lanceolate, ovate or suborbicular, tomentulose, hirsute, sericeous-tomentose, ciliate or subglabrous, hairs stellate, forked or simple, 0.05–2.0 mm. long; petiole 0.3–14.5 (–20.5) cm. long.

Lamina 3.1–24 (–30) cm. long, 1.1–21.5 (–27) cm. wide, usually broadly ovate, sometimes lanceolate, rarely elliptic, the base rounded to cordate, rarely cuneate or truncate, the apex acute, rarely acuminate or rounded, the upper surface tomentulose, sericeous-tomentulose, canescent and woolly or velvety to the touch, or glabrous, hairs stellate and usually also forked and simple, 0.05–1.2 mm. long, sometimes also minute resin-colored granules scattered over the surface, the lower surface with similar indument but never completely glabrous, the margin usually irregularly crenate to serrate, crenations or serrations 0.9–8.3 mm. wide, 0.3–3.0 mm. high, 5–10 pairs of primary veins, 1–3 are basal.

Inflorescences loose or compact, 2.5–21.5 (–39) cm. long, in axils of 1–6 upper leaves, sometimes apparently also terminal, rarely leaf-opposed or 90° from a leaf axil, or not associated with a leaf, corymbiform, branched, the ultimate divisions umbellate, the umbels 2–5-flowered, the flowers numerous, moderate or few, sometimes fragrant, the peduncle 2–11 (–16) cm. long, usually with a primary branch 0.4–5.2 (–7.0) cm. long, often with a secondary one 0.3–2.0 (–4.0) cm. long, and sometimes with a tertiary one 0.5–1.6 (–3.0) cm. long, and rarely with a quaternary one to 2 cm. long, the pedicel 0–7 mm. long; bracts sometimes soon deciduous, rarely 2 united, 1.0–5.5 (–10) mm. long, 0.1–3.0 (–14) mm. wide, ovate, lanceolate, or deltoid, rarely linear, apex usually acute, sometimes rounded, tomentulose, hirsute or ciliate, hairs stellate, sometimes also forked and simple, 0.1–0.4 (–1.3) mm. long.

Calyx sometimes orange to bright red, pinkish brown or yellow green, 3.5–9.0 mm. long, 3.8–10 mm. wide, tomentulose, sometimes also sericeous, hairs stellate, sometimes also forked, simple, or glandular, 0.05–0.5 (–1.5) mm. long, the teeth 1.2–5.5 mm. long, 1.3–4.8 mm. wide, deltoid to ovate, acute or acuminate, the sinus acute to narrowly rounded; petals usually pink to red, sometimes white to yellow, rarely pale blue, pale purple, violet, or lilac with a proximal orange spot, 5.0–9.0 (–15.5) mm. long, 1.6–5.0 (–7.5) mm. wide, obovate, oblanceolate, elliptic, oval, ovate or oblong, the apex usually

rounded, rarely emarginate, the base acute, attached to stamens for 0.8–3.0 mm., the claw 0.5–3.0 mm. long; sometimes glandular tissue present with lobes extending between the bases of the petals.

Longistylous form. Stamens 4–6 mm. long, the filaments often yellow, sometimes rose, united up to the anthers or free for 0.2–2.0 mm., the anthers yellow, 1.2–2.2 mm. long, 0.6–1.4 mm. wide, oblong, emarginate at both ends, usually deeply so at the apex; pistil 5.2–9.0 mm. long, the styles filiform, often slightly clavate, papillose for 0.6–2.0 mm. at the apex, free for 2.9–6.0 mm., to the ovary, or united for 0.5–1.0 mm., the ovary ovoid or elliptic, the ovary and base of styles usually densely sericeous, sometimes tomentose or hirsute, hairs simple, forked, and sometimes also stellate, 0.5–1.8 mm. long, the carpels sometimes 6-8, stipe none.

Brevistylous form. Stamens 4.7–8.1 mm. long, the filaments free for 1.8–5.0 mm., the anthers 1.0–2.5 mm. long, 0.7–1.4 mm. wide, rarely staminodes present, 0.1–0.2 mm. long; pistil 3.6–5.3 mm. long, the styles filiform, papillose for 0.6–0.8 mm., free for 1.4–2.6 mm., usually to the ovary, sometimes united for 1 mm., the ovary globular or ovoid, usually densely sericeous, sometimes sericeous-tomentose or hirsute, hairs simple and forked, 0.7–1.7 mm. long, the carpels sometimes 6–8, stipe none.

Fruit a green, brown or purplish-red capsule, ovoid or oblong, 4–10.5 mm. long, of which the arista is 0–2.0 (–3.0) mm. long, 4–9.4 mm. wide, the dorsum of carpels obtuse or subacute, the sulci between the carpels in the distal half of the fruit or extending for its entire length, shallow or deep, extending a fifth to half way to the center of the fruit, tomentose, tomentulose, or sericeous, hairs simple, forked, and stellate, the last short, 0.1–1.6 mm. long, the stipe (base of capsule) 0–1 mm. long; dehiscence all along the ventral sutures, sometimes also a fifth to half way along the dorsal sutures and partly septicidal; seeds 1 or 2 per cell, the body brown, trigonal, 1.8–3.5 mm. long, 1.1–2.0 mm. wide, sometimes testa loosened for 0.2–0.5 mm., or with an arista 0.7 mm. long, or with an ascending wing 0.3–5.3 mm. high, 0.7–3.0 mm. wide, obliquely deltoid or adaxial edge straight and abaxial edge convex, the apex rounded or acute.

A few species produce flowers and fruit throughout the year, others have a restricted flowering and fruiting period.

TYPE: *Melochia umbellata* (Houtt.) Stapf.

DISTRIBUTION: India and Southeast Asia, Indonesia, the Philippines, and other Pacific islands to the Tuamotu Islands, in forests, thickets, and disturbed areas, under wet or dry conditions, on soils or rocks of calcareous or volcanic origin, at 0–1,400 (–1,700) meters elevation.

1. Melochia umbellata (Houtt.) Stapf, Kew Bull. 317. 1913.
Visenia umbellata Houtt. Handleidung 8:309. 1777.
Wisenia indica Gmel. Syst. 2:515. 1791.
Riedleia tiliaefolia DC. Prod. 1:491. 1824.
Riedleia velutina DC. Prod. 1:491. 1824.
Aleurodendron album Reinw. Sylloge Pl. Ratisbonn, 2:12. 1828.
Glossospermum velutinum (DC.) Wall. Cat. n. 1153. 1829.
Pentaglottis tomentosa Wall. Cat. n. 1156. 1829.
?Glossospermum ?cordatum Wall. Cat. n. 1155. 1829.
Melochia arborea Blanco, Fl. Filip. 524. 1837.
Hypericum pentandrum Blanco, Fl. Filip. 614. 1837.
Visenia Javanica Jungh. *in* Hoev. & DeVriese, Tijdschr. 7:302. 1840.
Riedleia Aleurodendron (Reinw.) Steud. Nom. ed. 2, 2:459. 1841.
Riedleia cordata (Wall.) Steud. Nom. ed. 2, 2:459. 1841.
Riedleia Wallichiana (Wall.) Steud. Nom. ed. 2, 2:460. 1841.
Visenia alba (Reinw.) Endl. ex Walp. Rep. 1:351. 1842.
Visenia tomentosa Miq. Anal. Bot. Ind. 3:4. 1852.
Visenia velutina (DC.) Turcz. Bull. Soc. Nat. Mosc. 31(1):212. 1858.
Melochia velutina Wall. ex. Bedd. For. Man. Bot. 35. 1869 or 1871.
Melochia indica Kurz, Prelim. Rep. For. Veg. Pegu, App. A, 23. 1875.
Melochia indica var. *deglabrata* Kds. & Val. Bijdragen tot de Kennis der Boomsoorten van Java 2:194. 1895.
Melochia odorata var. *Schlechteri* Mildb. Engl. Bot. Jahrb. 62:350. 1929.

Usually a small tree, sometimes a shrub, 2–15 (–20) meters high, 4–15 (–35) cm. in diameter, the ramification ascending to horizontal, the bark about 4 mm. thick, rather smooth to rough, pale brown to dark grey brown, with some longitudinal ridges, the wood straw, the young stems and petioles woolly to the touch, tomentulose, hairs stellate, 0.1–1.0 mm. long, often yellowish brown at base, the internodes 1–7 cm. long; stipules deciduous, 4.3–10 mm. long, (1.1–) 5–12 mm. wide, ovate to suborbicular, the apex usually rounded, covered with simple, forked and stellate hairs 0.1–0.5 mm. long; petiole 2.5–11 (–20.5) cm. long.

Lamina 6.3–14.8 (–30) cm. long, (2–) 3.8–14 (–27) cm. wide, usually broadly ovate, the base rounded to cordate, the apex acute, often lanceolate and much reduced just below the inflorescence, both surfaces of young leaves covered with stellate hairs, rarely also simple and forked, 0.1–0.5 mm. long, woolly or velvety to the touch, larger hairs sometimes yellow brown at base, often minute resin-colored granules scattered on surface, young leaves somewhat canescent, older ones glabrescent, the margin irregularly crenate-serrate, serrations 1.8–6.0 mm. wide, 0.5–3.0 mm. high, 7–10 pairs of primary veins, 2 or 3 are basal.

Inflorescences fairly loose, in axils of upper 3 or 4 or more leaves, 3.7–16 (–39) cm. long, corymbiform, the flower number moderate, the ultimate divisions umbellate, the umbels 3–5-flowered, the peduncle (2.8–) 4–6.5 (–11) cm. long, with a primary branch 0.5–2 (–5.5) cm.

long, a secondary one 0.5–2(–4) cm. long, sometimes a tertiary one 0.5–1.3 (–3) cm. long, rarely a quaternary one to 2 cm. long, the pedicels 1–3 mm. long; bracts (1–) 2.5–5.3 (–10) mm. long, 0.7–2.3 (–14) mm. wide, ovate to lanceolate, the apex rounded or acute, covered with stellate hairs 0.1–0.3 mm. long.

Calyx yellow green to pinkish brown, 4.8–6.2 (–7.0) mm. long, 4–5.7 mm. wide, covered with stellate hairs 0.1 mm. long, and less numerous simple, forked, and stellate hairs to 0.6 mm. long, the teeth 2–3.4 mm. long, 1.4–3.3 mm. wide, deltoid to ovate, acute or slightly acuminate, the sinus acute; petals usually pink (light pink to red), sometimes white to yellow and sometimes orange proximally, rarely pale blue, pale purple or violet, (5.5–) 6–7.2 mm. long, (1.9–) 2.2–3.7 mm. wide, obovate, oblanceolate, or elliptic, attached to the stamens for 1–2 mm., the claw 0.5–1.5 mm. long, usually glandular tissue present with lobes extending between the bases of the petals; filaments and styles cream, anthers yellow.

Longistylous form. Stamens 4–4.9 mm. long, the filaments united up to the anthers or free for 0.2–0.9 mm., the anthers 1.2–1.6 mm. long, 0.8–1.0 mm. wide, oblong, slightly narrower at apex, emarginate at both ends, almost to the middle from the apex; pistil (6.2–) 6.6–7.6 mm. long, the styles free for (3.5–) 4.2–5.2 mm., united for 0.5 mm., papillose and clavate for (1–) 1.3–1.7 mm. at the apex, the base hirsute, the ovary ovoid, pentagonal, densely hirsute or sericeous, hairs forked, simple, and stellate, 0.5–1.3 mm. long, stipe none.

Brevistylous form. Stamens 5.5–6.4 mm. long, the filaments free for 3.3–5.0 mm., the anthers 1–1.2 mm. long, 0.7–1.0 mm. wide; pistil 4.6–5.2 mm. long, the styles free for 1.8–2.5 mm., nearly to the ovary, papillose for 0.6 mm., the ovary densely hirsute, hairs mostly forked and simple, to 1 mm. long, stipe none.

Fruit green, brown or purplish red, 8–9.5 mm. long, 6.3–7.5 mm. wide, oblongish, only slightly narrower at the apex, the sulci between the carpels deep, extending nearly half way to the center of the fruit at both apex and base, the sides of the carpels cohering only for a very short distance at the base, covered with stellate hairs 0.1 mm. long and simple, forked, and stellate hairs 0.5–1.0 mm. long, the stipe 0–0.5 mm. long; dehiscence along the ventral sutures; seeds winged, the body brown, 2–3.3 mm. long, 1.5–2.0 mm. wide, the wing ascending, 4–5.3 mm. high, 2–3 mm. wide.

Flowering and fruiting specimens collected throughout the year, peak of flowering May–August, fruiting June–August.

TYPE LOCALITY: East Indies, probably Java.

DISTRIBUTION: Indigenous from India to New Guinea, often common in secondary thickets, in recent clearings, along the edges

of forests and rivers, often in red calcareous soil, often in localities affected by monsoons, at 0–1,400 (–1,700) meters elevation.

INDIA: TERR. CANARA (KANARA): Mercara and Dharwar, ?*Metz* 623a (S). Car Nicobar, *Prain* March 1891 (US).

INDOCHINA: AUSTRA-CHOCHINCHINAE: Dinh ad Baria gallicae, *Pierre* 544 (L, ?US). TONKIN: Rive droite de la rivière Novie entre C. Thap. et les roches de Notre-Dame, *Balansa* 3719 (L). ANNAM: Dabac, Hout Donai, *Poilane*, s.n. (S).

MALAYA: PERAK: *Dr. King's Collector* 8401 (L). Kampong Tembok, 3 mi. N. of Ipoh, *Sinclair* 9854 (L). ?PERAK: *Father Scortechini* s.n. (US). SELANGOR: Kepong Plantation, *Symington* Kepong Field No. 32872 (L). PAHANG: Sabai Estate, Bentong, Kemanshul Div., *Shah* 258 (L).

IND. OR. HERB. *Wallich* 1156 (L). Isotype of *Pentaglottis tomentosa* Wall.

SUNDA ISLANDS: SUMATRA: Singarong agong, *Robinson & Kloss* May 24, 1914 (US) ?Indrapoera, *Korthals* s.n. (L). Malintang, *Bunnemeijer* 3793 (L). SIBOLANGIT: Karohoogvl by Sarinembah, *Galoengi* 16 (L). BERKOELEN: Kebanagoeng, *de Voogd* 1200 (L). Djambi. S. Lesing by Pahoe, *Posthumus* 1015 (L), 1059 (L). TAPIANOELI: TOBA: Toetoepan, *Boeea* 5978 (L). Toba, *Duwchond* 252 (L). Near Taroentoeng, *Bartlett* 8367 (L, US). Palembang, Bamas, *Grashoff* 170 (L), 1091 (L). ?Paoe Palembang, *Forbes* 2546 (L). N. SUMATRA: Deli, Padang and Bedagei to Bila, Karohochebene, bei Jongging, am NW. Toba See, *Lörzing* ?1758a (L), 7987 (L), 8075 (L), 15058 (L), 15965 (L). WEST COAST: Koerintjo Bt. te Bakar, *Binnemeyer* 8174 (L). CENTRAL SUMATRA: Mt. Sago near Pajakumbuh, *Maradjo* (*ass. W. Meijer*) 14 (L). EAST COAST: Padang, *Stomps* 11–10–1923 (L). ASAHAN: Peddaloeng, *Bartlett & LaRue* 136 (L), 139 (L). Hoeta Padang, Asahan, *Krukoff* 4421 (L, US). Adian Rindang, Asahan, *Boeea* 8726 (L). Vicinity of Loemban Ria, Asahan, Hoeta Bagasan, *Boeea* 6863 (S, US), 7287 (US), 7530 (S), 7902 (S, US). LABOEHAN BATOE: Kota Pinang, Langga Pajoeng on the Soengei Kanan, *Toroes* 3636 (L, S, US). Si Mandi Angin on the Soengei Kanan, *Toroes* 3957 (US). KRAKATAU (KRAKATOA): *Brenlage* s.n. (L). P. Rakata, SE. side, *v. Borssum Woolkes* 1024 (L). Verlaten Eiland, *Backer* s.n. (L). JAVA: ?*Waitz* s.n. (L). *Junghuhn* 408 (L). *Zollingero* 34 (L). *H. Lugo Batar* s.n. (S). ?*Reinwardt* 2350 (S). East Java, *Reinwardt* s.n. (S). *Schierbrand* s.n. (W). Tjibodas, *Raap* 766 (L). G. Malabar Poentjak gede, *Monterie* 40 (L). Montis Sebu, Sorū, *Junghuhn* s.n. (L). Bagelen, *Vorderman* s.n. (L). Bandoeng, *Popta* 542/98 (L). Meester Cornelis, *Backer* s.n. (L) Solak, *Möller* s.n. (S). Buitenzorg and vic., *Danser* 5573 (L), *Sutrisno* 25 (L), *Schuurman* 33 (L), *Soegandiredja* 233 (L), *Durand* 818 (L). BANTAM: TJIMARA: Oedjoeng, *Koorders*, 7744 β* (L). G. Pangissan, *Koorders* 7744 β (L). G. Karang, *Koorders* 7743 β (L). Batavia, *Koorders* 30901 β (L), *Backer* 88 (L). Res. Batavia G. Salak, *Koorders* 24411 β (L). Depok, *Hallier* Aug. 24, 1896. BANEAN: Tandjoeng Tajar, *Karta* 148 (L). Soerabaja, *Doyeli* 383 (L), 786 (L), 950 (L). Paroeroean, *Backer* 7810 (L), 37444 (L). P. Purmerend, middle of the island, *den Hoed* 3063 (L). Japara, Soemanding, *Neth. Ind. For. Service* Ja: 3724 (L). MADIOEN: Pandan, Kendeng, Trinil, *Elbert* 447 (L), 506 (L). Lawoe, Djogolaranga, Oosbooch, Kali Djeplog, *Elbert* 278 (L). Vak 112 houtrestery Toeloeng, *Wind* 6289 (L). G. Wilis Ngebel, *Koorders* 7746 β (L). PROV. PREANGER: *Ploem* s.n. (L). Takoka, *Koorders* 15155 β (L). SEMARANG: Kedoengdjati, *Koorders* 7740 β (L), 7745 β (L), 7748 β (L), 7749 β (L). Pangentjongan, *Koorders* 7742 β (L), 14024 β (L). Palaboean ratoe, *Koorders* 7738 β (L), 7739 β (L), 7741 β (L). Telomojo, *Koorders* 27970 β (L). Karangasem, *Koorders* 7747 β (L). Tjiratjap Djampang koelon, *Backer* 17394 (L). Reg. Tjadas

Malang bij Tjidadap. L. v. Tjibeber Pasir Anger, *Winckel* 113 β (L), 161 (L), 1356 β (L), Bat. huizen *v/d Brink* 99a (L). Tjatjaban, and in the ravine of the river Tji Taroem, *Hochreutner* 1667 (L). Res. Semarang. Telomojo, *Koorders* 27970 β (L). Res. Kedoe G. Sendoro, *Koorders* 11354 β (L). Res. Besoeki Poeger, Banjoewangi, *Koorders* 7753 β (L), 7756 β (L). Prov. Banjumas. Prin-gambo, *Koorders* 7752 β (L), *Koorders* 37048 β (L). Res. Besoeki Rogodjampi, *Koorders* 29088 β (L). Res. Kediri. N. v. Tritik grens Kediri-Rembang, *Thorenaar* 102 (L). Pekalongan. Soebah, *Koorders* 11608 β (L), 11609 β (L). Southeast Java, *Forbes* 1343 (L). CENTRAL JAVA: G. Muria, Tjollo, N. of Kudus, *Kostermans* 6264 (K, L). WEST JAVA: 18 km. S. of Rangkasbitung, *Buwalda* 2855 (L). ?Java, *Tjiomas* 28/11/88 (L). BORNEO: *Winkler* 2197 (L). ?G. Kunepay, *Hallier* 1939 (L). ?Dversin, *Korthals* s.n. (L). Rajang, Sibu Kalong, *Haviland* 2836 (L). NORTH BORNEO: Kinabalu Mt., *Puasa* N. Borneo Forestry Dept. No. 1541 (L). Tambunan, *Wyatt-Smith* Kepongfield No. 80412 (L, US). Kampong Kinasaraban, *Sinclair* et al. 8994 (L). CELEBES: *de Vriese & Teijsmann* s.n. (L). TUKANG-BESI ISLANDS: Biriongko, *Elbert* 2588 (6083) (L). Kp. Palima, *Noerkas* 265 (L). Bonto Djai, *Rachmat* Exp. v. Vuuren 29 (L). Malili, Thawata, Boschproefstation #Cel/V–164 (L). Rante Lemo, Pare-Pare, *Kjellberg* 3827 (S), 3827a (S). Labibia, *Kjellberg* 1363 (S). Makale, *Kjellberg* 1656 (L, S). G. Bontham, *Bünnemeyer* 12354 (L). Minahassa, *Koorders* 18091 β (L), 19718 β (L); Menado, *Koorders* 18089 (L). SOUTHEAST: Landschaft Lankape, *Elbert* 7420 (3029) (L). Landschaft Rumbia, *Elbert* 7528 (3071) (L). BUTON ISLAND: Lipumangau, *Elbert* 6502 (2745) (L). Limbo, *Elbert* 6616 (2785) (L). MOENA (MUNA) ISLAND: Raha, *Elbert* 7086 (2904) (L), Boschproefstation 1 1 5848 (L). Tanette, *Bünnemeyer* 11760 (L). SW. CELEBES: KAMP: Biroro by Lombasang, *Bünnemeyer* 11646 (L), 11456 (L). LOMBOK: Rindjani-Vulkangebirge, N. side Labuan tjarik, *Elbert* 235 (535) (L). SW. LOMBOK: Plambi, *Elbert* 5763 (2411) (L). SUMBA (SOEMBA): Maomarroe, *Iboet* 486 (L), 538 (L), Lologooh, *Iboet* 278 (L). WEST SUMBA: Waikalubah, *Monad de Froidville* 1869 (L). FLORES: Endeh, *Jaag* 1806 (L). ALOR: Central highland, Lantoka-Pido, *Jaag* 1245 (L). TIMOR: A specimen ex Herb. Mus. Paris, labeled *Riedleia tiliaefolia* (US 13124). *Zippelius* s.n. (L). En Onderh. P. Alor, *Bowman-Houtman* 159 (L). *A. de Jussieu* missit 1834 (S), ?*M. umbellata* or *M. odorata*. E. TIMOR: Plateau of Baucau, *Van Steenis* 18048 (L).

PHILIPPINES: *Hallier* 347a (L). PALAWAN: Fanabay, *Manalo* 3 (Forestry Bur. #7426) (US). TAWITAWI: Sulu Prov., *Ramos & Edaño* Bur. Sci. #44111 (L). MINDANAO: ZAMBOANGA: Tetuan, *Ahern* 48 (US). DAVAO: Todaya (Mt. Apo), *Elmer* 10864 (L, US), *Clemens* Bur Sci. #15581 (L); Santa Cruz, *Williams* 2799 (US). AGUSAN: Cabadbaran (Mt. Urdaneta), *Elmer* 13651 (L). Surigao, *Ahern* 340 (US). NEGROS: NEGROS ORIENTAL: Dumaguete (Cuernos Mts.), *Elmer* 9493 (L, US). SIARGAO: *Ramos & Pascasio*, Bur. Sci. #34853 (L). LEYTE: *Wenzel* 1352 (L). SAMAR: *Ramos* Bur. Sci. #17594 (US). CULION: *Merrill* 619 (US). MINDORO: Baco River, *McGregor* 299 (US). Calapan, *Escritor* Bur. Sci. #21269 (L, US). Mt. Yagaw, SE. slope, *Conklin* 269 (L, US). East Mindoro, 18 km. S. of Puerto Galena, San Teodoro, *Vera Santos* 5291 (L, US). LUZON: Morong, Tanay, *Merrill* 2286 (US). SORSOGON: Irosin, Mt. Bangko, *Edaño & Gutierrez* 161 (L); Mt. Bulusan, *Elmer* 16505 (L, S, US); Patag, *Sinclair & Edaño* 9613 (L). Batangas, *Ramos & Deroy* Bur Sci. #22665 (US). LAGUNA: Los Baños, *Quisumbing* 466 (US), *Ramundo* s.n. (S); Mt. Maquiling, *Elmer* 17920 (L, S, US), *Mendoza* Phil. Nat. Herb. 12201 (US). RIZAL: *Ramos* 1086 (US); *Ahern's Collector* Forestry Bur. #3152 (US); Manila, Navaliches, *Loher* 155 (US); Montalban, *Loher* 5574 (US); Bosoboso, *Merrill* 2829 (US), 2840 (US). BATAAN: Dinalupijan, *Merrill* 1476 (US). ZAMBALES: Subig, *Hallier* 4347 (L). TAYABAS: Casiguran,

Mearns Bur. Sci. #2972 (US). BENGUET: Sablan, *Elmer* 6086 (US). CAGAYAN: Littoc, Lagum, vic. of Peñablanca, *Adduru* 161 (US), 228 (US).

MOLUCCAS: TALAUD: Karakelong, *Lam* 2570 (L). MOROTAI: *Kostermans* 1541 (L). HALMAHERA: *Idjan & Moehtar* 365 (L). Kmp. Goal., *Pleyte* 157 (L). S. peninsula, *Anang* 553 (L). TERNATE: Kabora, *Anang* 135 (L). Foramadiahi, *Beguin* 1103 (L), 1594 (L). Lagoena, *Beguin* 628 (L). Dessa Takome, *Bish.* 23 (L). East coast, *Pleyte* 82 (L). SOELA (SULA): Sanana, Tandjong Baliha, *Bloembergen* 4367 (L). Mangoli Island and N. of Mangoli, *Neth. Ind. For. Serv.* bb. 29860 (L). BURU (BOEROE): *de Vriese* Feb. 1860? (L). AMBOINA (AMBON): Poka, exp. v. Hulstyn, *Saanan* 105 (L). KAI (KEI): Ohoitiel bij Toeal, *Jensen* 312 (L). AROE (ARU): P. Trangan, KP. Ngaibor, *Buwalda* 5334 (L). TANIMBAR: *Neth. Ind. For. Serv.* bb 24350 (L). BABAR: PULAU WOTAN: E. Herloh, *van Borssum Waalkos* 3028 (L).

NEW GUINEA: Near Kp. Saban (Wentholt exp.), *Anta* 261 (L). Jappen-Biak, Mentembae, *Aet & Idjan* 104 (L). JAPEN: Seroei, *Neth. Ind. For. Serv.* bb. 30566 (L). RADJAH AMPAT: Batanta Island, W. of Sorong, Marchesa Bay, Amdoei village, *van Royen*, 3533 (L). Sorong, Misool, W. of Fakal, bank of Kasim River, *Pleyte* 1128 (L). Hollandia (Hamadi) Onderafd. Hollandia, *Kalkman* #BW3677 (L). Stephansort, (?*M. umbellata*, fruit immature), *Lewandowsky* 34 (L, S). PAPUA: *Schlechter* 16143 (L, S), isotypes of *M. odorata* var. *Schlecteri* Mildb.; Koitaki, *Carr* 12672 (L); Lake Daviumbu, Middle Fly River, *Brass* 7734 (L); Northern Dist., ca. 3 mi. from Aku on Kuruaku tract Tufi subdist., *Saunders* 30 (K, L); MILNE BAY DIST.: Cape Vogel peninsula near Tapio village, *Hoogland* 4288 (A, L).

HAWAII: OAHU: Kahuku mauka, *Lam* 7285a (L), *Degener* et al. 19548 (L, S, US).

This species can be distinguished from the other species in the section *Visenia* by its oblong fruit with intercarpellary sulci extending its entire length, large suborbicular stipules, and relatively large-winged seeds.

2. Melochia odorata L. f. Supp. Plant. 302. 1781.

A shrub or spreading, umbrella-crowned tree (1.2–) 3.3–15 meters high, 9–10 cm. in diameter, the young stems and petioles rather densely puberulous, hairs stellate and forked, 0.1–0.5 mm. long, the internodes 0.3–3.0 cm. long; stipules deciduous, 2.5–4.0 (–9.0) mm. long, 0.8–1.1 (–4.0) mm. wide, deltoid-acute or deltoid-acuminate, covered with forked, stellate, and simple hairs 0.1–0.3 mm. long; petiole 1.0–9.0 cm. long.

Lamina 4–20.7 cm. long, 2–18.7 cm. wide, usually ovate, the base rounded to cordate or truncate, the apex acute to acuminate, leaves subtending the inflorescence sometimes lanceolate-ovate, the base cuneate to rounded, and at the lower end of the range in size, both surfaces of young leaves silvery to greenish- or tan-canescent, densely puberulous, sometimes rough, hairs stellate, forked, and simple, 0.1–0.5 mm. long, soon glabrate, a few scattered hairs remaining, especially on the veins, the margin irregularly crenate-serrate, serrations 1.7–6.6 mm. wide, 0.5–2.4 mm. high, 6–10 pairs of primary veins, usually 2 (1–3) are basal.

Inflorescences usually loose, 2.5–7.0 (–14) cm. long, in axils of upper 2–4 leaves, corymbiform, the flower number moderate, the ultimate divisions umbellate, the umbels 3–5-flowered, the flowers scented, the peduncle 2.5–4.5 (–13) cm. long, with a primary branch 0.8–1 cm. long, and sometimes a secondary one 0.5–0.8 cm. long, the pedicels (1–) 2–7 mm. long; bracts 3.7–5.5 mm. long, 0.5–1.7 mm. wide, lanceolate, covered with stellate and forked hairs 0.1–0.4 mm. long.

Calyx pink or pale purple, 5.8–8.6 mm. long, 6.1–8.0 mm. wide, densely covered with forked, stellate, and simple hairs 0.1–0.5 mm. long, the teeth 3.7–5.0 mm. long, 2.5–3.0 mm. wide, deltoid or ovate, acuminate, the sinus acute; petals usually pink, rarely pale lilac, pale lilac with a proximal orange spot, cream with yellow proximally, or white, 7.8–12.5 mm. long, 3.0–4.2 mm. wide, ovobate, the claw 1.3–1.7 mm. long, attached to the stamens for 1.4–2.5 mm., undulating ring of glandular tissue 0.2 mm. wide between the calyx and corolla ascending between the petals and descending at their bases.

Longistylous form. Stamens 5–5.5 mm. long, the filaments free for 1.3–1.5 mm., the anthers 1.5–1.7 mm. long, 1.0–1.2 mm. wide, oblong, usually emarginate at both ends, usually deeply so at the apex; pistil 7.5–8.2 mm. long, the styles 4.5–5.7 mm. long, free to the ovary, papillose and clavate at the apex for 1–1.5 mm., the ovary elliptical to ovoid, densely sericeous, hairs 0.5–1.5 mm. long, the carpels sometimes 7 or 8, stipe none.

Brevistylous form. Stamens 6.5–6.8 mm. long, ?staminodes 0.1 mm. long sometimes present, the filaments free for 3.7 mm., the anthers 1.5–1.6 mm. long, 0.8–0.9 mm. wide; pistil 4.5 mm. long, the styles 2.5 mm. long, free to the ovary, the carpels sometimes 6 or 7.

Fruit ovoid, 4–6 mm. long, 4–6.5 (–8.0) mm. wide, the arista remnant of styles 0–2.0 mm. long, the sulci between the carpels shallow to fairly deep, sericeous to tomentulose, hairs 0.5–1.5 mm. long; dehiscence all along the ventral sutures and a third to half way along the dorsal sutures, very slightly septicidal; seeds 1 or 2 per carpel, 1.9 mm. long, 1.1 mm. wide, red brown, wing or other projection usually absent, sometimes with a wing 0.6–2.0 mm. high, 1.0 mm. wide.

Flowering specimens collected throughout the year except in January; fruiting ones throughout the year except in January, May, September, and December.

TYPE LOCALITY: Tanna Island, New Hebrides.

DISTRIBUTION: New Guinea to New Caledonia, common in second growth rain forest, at the edge of the rain forest, along river banks, in savanna, littoral, in disturbed ground, on limestone or sandy soil, at 0–1,200 meters elevation.

NEW GUINEA: MADANG: Near Mawan village, Gogol Valley (ca. 25 km. inland), *Hoogland* 4917 (A, L, US). Yllabe by Finschhafen, *Weinland* 254 (L, US). Cycloop-gebergte. W. van Ifor orderafd. Hollandia, *Kalkman* 3504 (L). MOROBE: Lae, *Dept. Forests Native Collector* 5494 (L); Busu River near Lae, *White* N.G.F. 9550 (L); Bupu River, near Lae, *Millar* N.G.F. 9298 (L); Manum Waters on the Nadzab Road, *Womersley & Floyd* 5655 (L); Sattelberg, *Clemens* 521 (L). PAPUA: Daru Island, Western Division, *Brass* 6346 (L). Kokoda, *Carr* 16277 (L). Isuarava, *Carr* 16041 (L). Rouna, *Carr* 12405 (L). ROSSEL ISLAND: Abaleti, *Brass* 28336 (L, US); Jinju, *Brass* 28533 (L, US). MILNE BAY: Biniguni Camp, Gwariu River, *Brass* 23931 (A); Between Dabora and Wabubu, Cape Vogel Peninsula, *Brass* 21871 (A); Peria Creek, Kwagira River, *Brass*, 23995 (A).

SOLOMON ISLANDS: BOUGAINVILLE: Kieta, *Kajewski* 1539 (L); Kugimaru, Buin, *Kajewski* 1797 (L). NEW GEORGIA: *Waterhouse* 131 (K). GUADALCANAL: Nalimbu River, *F. S. Walker & White* B.S.I.P. 17 (L); Vulolo, Tutuve Mt., *Kajewski* 2539 (L); Neighborhood of Tenawe River and the sea, *Riley* 9 (US). SAN CRISTÓBAL: Waimamura, *Brass* 2681 (L).

NEW HEBRIDES: SANTA CRUZ ISLANDS: Vanikoro Island, *Kajewski* 555 (A, UC, US). Tanna and Nova Amsterdam, *Forster* in 1779 (S, W). ANEITYUM: Collector not mentioned, 61 (S); Anelgauhat Bay, *Kajewski* 713 (US).

LOYALTY ISLANDS: *Franc* 1093 (UC).

NEW CALEDONIA: *Prony* 1822 A (UC). *Deplanche* 155 (L). Slope of Ouen Toro, *McKee* 2247 (L, US). Chepenehe, *McKee* 5257 (L). Auf den Bergen bei Paita, 10 mi. from Nouméa, *Schlechter* 14978 (L). Near native village of Tribu Katricoin along trail northward from waterfall at fork of Bogen River and Table Unio, *Buchholz* 1289 (US).

This species is close to *M. vitiensis* and *M. aristata*. The seeds of *M. ordorata* are usually wingless, those of *M. vitiensis* are winged, and those of *M. aristata* are usually aristate. The young leaves of *M. odorata* are sometimes quite hairy, those of *M. vitiensis* and *M. aristata* are soon glabrate. The calyx and bracts of *M. odorata* are longer than those of *M. aristata* and *M. vitiensis*.

3. Melochia vitiensis A. Gray, Bot. U.S. Expl. Exped. 1:193. 1854.

A shrub to spreading tree 1.5–12 meters high, the young stems fuscous-tomentulose, hairs stellate, a few forked, 0.1–0.3 mm. long, the internodes 0.5–14.0 cm. long; stipules deciduous, 2.4–7.0 mm. long, 0.9–2.0 mm. wide, deltoid-acute to deltoid-acuminate, tomentulose, hairs stellate and forked, 0.1–0.4 mm. long; petiole 2–9.5 cm. long, indument similar to that on young stems but tending to occur on one side.

Lamina 6–17 cm. long, 3.3–12.0 cm. wide, broadly ovate, the base cordate, sometimes rounded to subtruncate in those subtending the inflorescence, the apex acute to acuminate, young leaves sericeous-tomentulose on both surfaces, hairs forked, simple, and stellate, older leaves subglabrate, with few, mostly stellate hairs 0.1–0.6 mm. long on the veins, the margin irregularly crenate-serrate, serrations 1.2–5.0 mm. wide, 0.3–2.5 mm. high, 7–10 pairs of primary veins, 2 or 3 are basal.

Inflorescences fairly loose, in axils of 1–4 upper leaves, 6–12.7 cm. long, corymbiform, the flower number moderate, the ultimate divisions umbellate, the umbels 2- or 3-flowered, the peduncle 6–9.5 cm. long, with a primary branch 0.8–3.8 cm. long, a secondary one 0.7–1.4 cm. long, and sometimes a tertiary one 1 cm. long, the pedicels 2.5–7.0 mm. long; bracts soon deciduous, 1.0–2.1 mm. long, 0.4–0.8 mm. wide, nearly linear to lanceolate and ovate, acute, densely tomentulose, hairs stellate, 0.1–0.2 mm. long.

Calyx 3.5–6.0 mm. long, 3.8–6.7 mm. wide, densely tomentulose, hairs stellate, 0.1–0.4 mm. long, the teeth 1.7–3.0 mm. long, 1.7–2.7 mm. wide, deltoid or ovate, acute, the sinus acute to narrowly rounded; petals pale yellow or white, 5.0–7.6 mm. long, 1.7–2.8 mm. wide, oval, elliptic, ovate or oblong, attached to the stamens for 1.5–2.0 mm., the claw 1–2 mm. long.

Longistylous form. Stamens 4.0–5.2 mm. long, the filaments united up to the anthers, the anthers bright yellow, 1.5–2.2 mm. long, 0.7–1.4 mm. wide, oblong, emarginate usually nearly to the middle from both ends; pistil 7.2 mm. long, the styles free for 3.5–4.5 mm., united for 1 mm., sparsely sericeous, hairs 0.3–0.7 mm. long, filiform, sometimes clavate, papillose for 0.6–1.0 mm., the ovary oblong, densely sericeous, hairs 0.7–1.4 mm. long, the carpels sometimes 6.

Brevistylous form. Stamens 4.7 mm. long, the filaments free for 1.8 mm., the anthers 2.0 mm. long, 0.9 mm. wide; pistil 4.3 mm. long, the styles free for 2.0 mm., united for 1 mm., filiform, the ovary globular, densely sericeous, hairs 1 mm. long.

Fruit 7.0–9.0 mm. long, 7.0–7.5 mm. wide, the arista 1–1.5 mm. long, globular-ovoid, pentagonal, the dorsum of carpels obtuse-angled, the sulci between the carpels extending a fourth to a third the way to the center of the distal half of the fruit, fuscous-sericeous-tomentose, hairs stellate (short), forked, and simple, 0.1–1.5 mm. long, the stipe 0–0.5 mm. long; dehiscence all along the ventral sutures and a third to half way along the dorsal sutures; seeds 1 or 2 per cell, winged, the body brown, 2.1–2.8 mm. long, 1.3–1.6 mm. wide, the wing extending 1.3–2.0 mm. beyond the body, 1.3–1.7 mm. wide, the adaxial edge straight, the abaxial edge convex, the apex rounded or acute.

Flowering specimens collected in March, July, October, and November; budding ones in May; fruiting ones in October and November.

TYPE LOCALITY: Fiji Islands: Vanua-levu, Somu-somu (on Taveuni), Ovalau, Oneata (Lau, eastern group).

DISTRIBUTION: Fiji Islands, in thin forest, thickets, clearings, crass-covered "forehills," on rocky limestone slopes and on low ground inside the sandy beach, at 0–500 meters elevation.

FIJI ISLANDS: U.S. South Pacific Exploring Exped. under Capt. Wilkes (GH, US 13128 lectotype). *Seemann* 37 (GH). VANUA LEVU: MATHUATA: S. slopes of Mt. Numbuiloa, E. of Lambasa, *A. C. Smith* 6549 (A, L, S, US). Lower Wainunu River valley, Mbua, *A. C. Smith* 1727 (GH, S. US). THAKAUNDROVE: Nakawanga, *Gressitt* 2487 (US). TAVEUNI: Vicinity of Waiyur, *Gillespie* 4701 (GH). KAMBARA (Lau group): *A. C. Smith* 1301 (GH, S, US). MATUKU: *Bryan* 259 (GH).

This species is closest to *M. odorata* and *M. aristata*. It is distinguished from them under the description of *M. odorata*. In addition, the leaf of *M. vitiensis* is usually broader and more frequently cordate at the base than that of *M. aristata*.

4. Melochia longepetiolata A. C. Sm. Journ. Arn. Arb. 31:310. 1950.

A tree 4–8 meters high, the young stems minutely tomentulose, hairs tan, stellate, 0.05–0.1 mm. long, the internodes 1–18.5 cm. long; stipules 3–5 mm. long, 0.8–2.0 mm. wide, deltoid-acute, minutely tomentulose, hairs stellate, 0.05–0.1 mm. long; petiole usually long, 2–19 cm. long, indument similar to that on young stems, a few hairs to 0.2 mm. long.

Lamina 6.2–24 cm. long, 3–21.5 cm. wide, usually broadly ovate, the base cordate, truncate or rounded, the apex acute, the upper surface glabrous, the lower surface subglabrous, hairs scattered, stellate, 0.1–0.2 (–0.4) mm. long on veins and in their axils, stellate hairs on the interstices 0.05 mm. long, the margin irregularly crenate to crenate-serrate, crenations or serrations 2.5–7.0 mm. wide, 0.5–1.9 mm. high, 6–10 pairs of primary veins, 2 or 3 are basal.

Inflorescences 17.5–21.5 cm. long, loose, in the axil of the uppermost leaf, sometimes not associated with a leaf or 90° from a leaf axil, at 1–2 nodes, few-flowered, corymbiform, the ultimate divisions umbellate, the umbels 2- or 3-flowered, the peduncle 7.5–11 cm. long, with a primary branch 3.5–5.2 (–7.0) cm. long, a secondary one 1–1.7 (–2.5) cm. long, and sometimes a tertiary one to 0.8 cm. long, the pedicels 5–7 mm. long; bracts deciduous, all fallen off.

Calyx 6–8.2 mm. long, 7.2–10.0 mm. wide, densely tomentulose, hairs stellate and forked, 0.05–0.2 mm. long, the teeth 4–5.5 mm. long, 3–4.8 mm. wide, ovate, acute, the sinus acute; petals salmon pink, 7.3–10.1 mm. long, 2–2.8 mm. wide, oblanceolate or obovate-elliptic, attached to the stamens for 1–2 mm., the claw 1–2.5 mm. long.

Longistylous form not seen.

Brevistylous form. Stamens 6.6–7.7 mm. long, the filaments free for 3.5–4.4 mm., the anthers 1.4–1.7 mm. long, 0.7–1.0 mm. wide, oblong, emarginate at both ends, staminodes sometimes present, 0.2 mm. long; pistil 7.2–7.5 mm. long (somewhat developed), the styles filiform, free for 2.6 mm., united for 1 mm., the base tomentose, the ovary globular, densely tomentose-sericeous, hairs 1.5 mm. long.

Fruit 8–9 mm. long, 7.5–8.0 mm. wide, the arista 1–1.5 mm. long, ovate, globular, obtuse-angled, the sulci between the carpels shallow, deepest distally, extending one-fifth of way to the center of the fruit, tomentose, hairs simple, forked, and stellate, 1–1.6 mm. long, also stellate 0.1 mm. long, the carpels sometimes 6–7, stipe none; dehiscence all along the ventral sutures and one-fifth along the dorsal sutures; seeds brown, winged, the body 2.6–2.8 mm. long, 1.6–1.7 mm. wide, the wing 2.5–3.0 mm. high, 1.1–2.0 mm. wide, the adaxial edge straight, the abaxial edge convex.

Flowering and fruiting specimens collected in October.

TYPE LOCALITY: Kandavu, Fiji Islands, type cited below.

DISTRIBUTION: Kandavu, Fiji Islands, in dense forest, or among reeds, at 200–500 meters elevation.

FIJI ISLANDS: KANDAVU: Mt. Mbuke Levu, *A. C. Smith* 218 (S, US, type). Hills above Namalata and Ngaloa Bays, *A. C. Smith* 110 (S, US).

This species can be distinguished from the other species with subglabrous leaves in the section *Visenia* by its long inflorescences, long peduncles, long petioles, and relatively large calyxes. Its salmon pink petals are also an aid to identification.

5. Melochia aristata A. Gray, Bot. U.S. Expl. Exped. 1:193. 1854.

A small tree 1.5–6.0 meters high, about 12 cm. in diameter, the young stems and petioles fuscous-tomentulose, hairs stellate, 0.1–0.2 mm. long, the internodes 0.7–8.3 cm. long; stipules soon deciduous, 2.4–4.0 mm. long, 0.8–1.5 mm. wide, deltoid or ovate, acute, densely hirsute-tomentulose, hairs fuscous, stellate and forked, 0.1–0.2 mm. long; petiole slender, 2–6 cm. long.

Lamina 5.5–12.0 (–15) cm. long, 2.0–8.9 (–12.4) cm. wide, broadly ovate, to lanceolate in leaf subtending the inflorescence, the base rounded, broadly subcordate, cordate, or nearly truncate, the apex acute or acuminate, the upper surface tomentulose, velvety to the touch, mostly stellate, to glabrate with hairs scattered, stellate, forked, and simple, 0.1–0.2 mm. long, the lower surface subglabrous with scattered stellate, forked, and simple hairs 0.1–0.4 mm. long, mostly on the veins, the margin irregularly crenate-serrate, serrations 1.3–5.6 mm. wide, 0.3–1.5 mm. high, 7–9 pairs of primary veins, 1–3 are basal.

Inflorescences 5–12 cm. long, fairly loose, the flower number moderate, in axils of 1–4 upper leaves, corymbiform, the ultimate divisions umbellate, the umbels 2–4-flowered, the peduncle 2.5–5.2 (–7.0) cm. long, with a primary branch 0.6–2.2 cm. long, a secondary one 0.5–0.8 (–2.2) cm. long, and sometimes a tertiary one 0.5 cm. long, the pedicels 1.5–3.0 mm. long in flower to 7.7 mm. in fruit; bracts soon deciduous, 2 mm. long, 0.5–1.5 mm. wide, ovate or lanceolate, acute, densely tomentulose, hairs stellate, 0.1–0.2 mm. long.

Calyx 4.0–5.5 mm. long, 4.1–6.5 mm. wide, tomentulose, hairs stellate, simple, a few forked, 0.1–0.4 mm. long, the teeth 1.6–3.0 mm. long 1.3–2.5 mm. wide, deltoid to ovate, acute, the sinus acute to narrowly rounded; petals red, pink, or white proximally and shading to rose distally, 7.8–9.0 mm. long, 2.0–3.6 mm. wide, obovate, oblanceolate, or elliptic, attached to the stamens for 2–2.8 mm., the claw 1–2.8 mm. long.

Longistylous form. Stamens 5.0 mm. long, the filaments free for 1.2–1.4 mm., the anthers 1.5–1.7 mm. long. 0.9–1.1 mm. wide, oblong, emarginate at both ends; pistil 8.2 mm. long, the styles slightly clavate, papillose for 0.8 mm., 5.0 mm. long, free to the ovary, the ovary ovoid, densely sericeous, hairs 0.6–1.0 mm. long.

Brevistylous form. Stamens 6.2–7.0 mm. long, the filaments free for 4.0 mm., the anthers 1.4–1.7 mm. long, 0.8–1.1 mm. wide; pistil 5.0 mm. long (slightly developed), the styles filiform, 2.6 mm. long, free to the ovary, the ovary globular-ovoid, sericeous-tomentose, hairs 0.7–1.1 mm. long.

Fruit 6.2–10.5 mm. long, of which the arista is 1–2 mm. long, 5.2–6.7 mm. wide, globular-ovoid, pentagonal, the dorsum of carpels obtuse-angled, the sulci between the carpels shallow, in the distal half of the fruit, extending a fifth to a fourth the way to its center, tomentose, hairs stellate (short), simple, and forked, 0.1–1.3 mm. long, the stipe 0–1.0 mm. long (base of capsule); dehiscence all along the ventral sutures and a third to half way along the dorsal sutures, slightly septicidal; seeds 1 or 2 per cell, wingless to slightly winged, the body 1.8–3.3 mm. long, 1.5–1.9 mm. wide, trigonal, brown, sometimes with an arista 0.7 mm. long, testa loosened for 0.2–0.5 mm., or with a wing 0.3 mm. high, 0.7 mm. wide.

Flowering specimens collected in March, May, July to September, and November; fruiting ones in March, May, and July to September.

TYPE LOCALITY: Upolu, Samoa, type cited below.

DISTRIBUTION: Samoa, Tonga, and Tuamotu Islands, in rain forest, thickets, in coral sand, at 0–650 meters elevation.

TONGA: VAVA'U ISLAND: Near Ngofe swamp, SW. side of the island, *Yuncker* 16029 (US). Vava'u and Lifuka, *Harvey* August and October 1855 (GH).

SAMOA: SAVAII: Safune, *Bryan* 140 (A). Vaipouli, *Vaupel* 360 (US). Near Fagalele, *Christophersen* 3403 (L). UPOLU: U.S. S. Pac. Exped. under Capt. Wilkes (GH, US, type). *K. & L. Rechinger* 1443 (US). Falefa, *Hochreutiner* 3449 (L). Ridge above Malololelei, *Christophersen* 164 (US). Id. Singamana, near Apia, *Hochreutiner* 3222 (L). TUTUILA: *Setchell* 512 (US).

TUAMOTU: MAKATEA: *Wilder* 1149 (A).

This species is close to *M. odorata* and *M. vitiensis*. It is distinguished from them under the description of *M. odorata*. In addition, the serrations of the leaves of *M. aristata* are generally shorter than those of the other two species.

6. Melochia degeneriana A. C. Sm. Journ. Arn. Arb. 31:307. 1950.

A slender tree 2–15 meters high, the young stems tomentulose or with scattered stellate and forked hairs 0.05–0.2 mm. long, the internodes 0.5–5.0 cm. long; stipules soon deciduous, 3.0–5.3 mm. long, 0.5–1.0 mm. wide, lanceolate, tomentulose to subglabrous, hairs stellate, 0.1–0.5 mm. long; petiole 0.3–3.0 cm. long, adaxial surface tomentulose, hairs stellate, 0.1–0.3 mm. long.

Lamina thin, 4–11.5 cm. long, 1.8–5.7 (–6.5) cm. wide, usually ovate, sometimes lanceolate-ovate, the base broadly rounded, rarely also narrowly rounded, the apex acute, both surfaces subglabrous, few scattered stellate, simple, and forked hairs 0.1–0.5 mm. long on the veins and sometimes also on the interstices, the margin irregularly and shallowly crenate-serrate, serrations distant, 1.3–8.3 mm. wide, low, 0.3–1.1 mm. high, 6–10 pairs of primary veins, 1 or 2 are basal, the second much stronger than the first.

Inflorescences fairly loose, the flower number moderate, sometimes few, in the axils of the upper 4 leaves, sometimes apparently terminal, or leaf-opposed, 6–14 cm. long, corymbiform, the ultimate divisions umbellate, the umbels 2–4-flowered, the peduncle 2.5–4.5 (–6.0) cm. long, with a primary branch 0.5–1.5 cm. long, a secondary one 0.3–0.5 cm. long, and sometimes a tertiary one to 0.5 cm. long, the pedicels 2.0–6.0 mm. long, densely tomentulose, hairs stellate, 0.1 mm. long and glandular, 0.2 mm. long; bracts soon deciduous, 1.1–1.6 mm. long, 0.4 mm. wide, lanceolate, tomentulose, hairs simple, forked, and stellate, 0.1 mm. long.

Calyx brownish pink 4.1–6.0 mm. long, 5.1–6.6 mm. wide, tomentulose, hairs stellate, 0.05–0.2 mm. long, sometimes also glandular, 0.2 mm. long, the teeth 1.2–3.1 mm. long, 1.6–3.1 mm. wide, deltoid, acute, the sinus acute to slightly rounded; petals pale yellow, 6.0–9.1 mm. long, 2.7–3.1 mm. wide, elliptic to obovate, attached to the stamens for 1.0–2.5 mm., the claw 1.0–2.5 mm. long.

Longistylous form. Stamens 5.2–5.5 mm. long, the filaments united up to the anthers, the anthers 1.8–2.0 mm. long, 0.9–1.4 mm. wide, oblong, emarginate at both ends, nearly to the middle from the apex; pistil 7.6 mm. long, the styles filiform, papillose for 1.5 mm., free for 5.0 mm., united for 1.0 mm., the ovary ovoid densely sericeous, hairs 0.7–1.0 mm. long, stipe none.

Brevistylous form. Stamens 5.5–7.0 mm. long, the filaments pale yellow, free for 2.5–3.5 mm., the anthers 2.1–2.5 mm. long, 1.3–1.4 mm. wide; pistil 4.0 mm. long, the styles 1.4–1.6 mm. long, free to the ovary, papillose for 0.8 mm., the ovary globular, densely tomentose-sericeous, hairs 1.0–1.2 mm. long, the carpels sometimes 6 or 7.

Fruit tough, 9–10 mm. long, of which the arista is 1.5 mm. long, 6–7.2 mm. wide, globular-ovoid, the dorsum of carpels obtuse-angled, the sulci between the carpels extending a fourth to half way to the center of the distal half, tomentose when young, hairs simple and forked, 0.3–1.2 mm. long, and stellate, 0.1 mm. long, stipe none; dehiscence all along the ventral sutures and a third along the dorsal sutures; seeds (immature) brown, winged, the body 2.3 mm. long, 1.3 mm. wide, the wing 1.3–3.0 high, 0.7–1.9 mm. wide.

Flowering specimens collected in January, May to September, and December; fruiting ones January to March, May to September, and December.

TYPE LOCALITY: Viti Levu, Fiji Islands, type cited below.

DISTRIBUTION: Viti Levu, Fiji Islands, in forest, often on dry crests, at 0–1,150 meters elevation.

FIJI ISLANDS: VITI LEVU: *Greenwood* 742 (K). MBA (formerly Tholo North): Western and southern slopes of Mt. Tomanivi (Mt. Victoria), *A. C. Smith* 5095 (L, US, type). THOLO NORTH: VIC. OF NANDARIVATU: Nauwanga, *Degener* 15399 (US). LAUTOKA: N. of Lomolomo, *Degener & Ordonez* 13643 (S, US). NANDRONGA AND NAVOSA (formerly Tholo West): Southern slopes of Nausori Highlands, *A. C. Smith* 4585 (L, S, US). Naduruloulou Agr. Exp. Garden, *Lam* 6933 (L). Namosi, *Gillespie* 2825 (US). Leviti Creek, Suva, *Mrs. Parham* 21 (A).

This species is closest to *M. mollipila*. The differences are given under the description of the latter species.

7. Melochia mollipila A. C. Sm. Journ. Arn. Arb. 31:308. 1950.

A branched shrub or small tree 3–7 meters high, the young stems densely fuscous-canescent, tomentulose, hairs stellate, 0.05–0.2 mm. long, the internodes 0.5–6.0 cm. long; stipules soon deciduous, 3.2–5.0 mm. long, 0.9–1.2 mm. wide, deltoid, acute, tomentulose, hairs stellate, 0.1–0.2 mm. long; petiole 0.5–6.0 cm. long, indument similar to that on young stems but hairs to 0.5 mm. long, average 0.2 mm.

Lamina 3.5–13.0 cm. long, 1.8–11.5 cm. wide, the small leaves being close to the inflorescence, usually broadly ovate, the base rounded to subcordate, rarely cuneate or subtruncate, the apex acute, the upper surface subglabrous, hairs few, scattered, stellate and forked, 0.1–0.2 mm. long, the lower surface slightly canescent, velvety to the touch, tomentulose, hairs stellate, 0.1–0.4 (most 0.2) mm. long, the margin irregularly and shallowly crenate or crenate-serrate, crenations or serrations 2–7 mm. wide, 0.3–0.8 mm. high, 8 or 9 pairs of primary veins, 2 are basal.

Inflorescences compact to fairly loose, the flower number few to moderate, in the axils of the upper 2 or 3 leaves and 3–9.5 cm. long, sometimes also terminal and 3.5 cm. long, corymbiform, the ultimate divisions umbellate, the umbels 2- or 3-flowered, the peduncle 2–4

(–5.5) cm. long, with a primary branch 0.4–1.4 cm. long and a secondary one 0.4–0.6 cm. long, the pedicels 1–3 mm. long in flower, to 5 mm. long in fruit; bracts soon deciduous, 2–3 mm. long, 0.7–1.0 mm. wide, deltoid, acute, tomentulose, hairs stellate, 0.1–0.2 mm. long.

Calyx pink, thick, 5.1–5.8 mm. long, 5.3–7.3 mm. wide, densely tomentulose, hairs stellate, fewer forked, 0.1–0.3 mm. long, the teeth 2.6–3.0 mm. long, 2.5–3.3 mm. wide, deltoid to ovate, acute, the sinus acute to somewhat rounded; petals pale yellow, 6.7–8.3 mm. long, 2.0–3.2 mm. wide, elliptic to oval, attached to the stamens for 0.8–1.5 mm., the claw 1–1.5 mm. long.

Longistylous form. Stamens pale yellow, 4.3–5.0 mm. long, the filaments united up to the anthers or free for 0.5 mm., the anthers 1.4–1.9 mm. long, 1.2–1.3 mm. wide, oblong, emarginate at both ends, sometimes fairly deeply so; pistil 6.3–6.7 mm. long, the styles filiform, papillose for 1 mm., free to the ovary, 3.5–4.0 mm. long, the ovary globular-ovoid, the ovary and base of styles sericeous-tomentose, hairs 0.5–1.2 mm. long, carpels sometimes 7–8, stipe none.

Brevistylous form. Stamens 6.2 mm. long, the filaments free for 4.0 mm., the anthers 1.6–1.7 mm. long, 1.0 mm. wide; pistil 4.5 mm. long, the styles 2.0 mm. long, filiform, free to the ovary, the ovary ovoid-globular, densely sericeous, hairs 0.7 mm. long, the carpels sometimes 6–8.

Fruit globular-ovoid, 5–7.5 mm. long, 5.3–9.4 mm. wide, the arista soft, 0.7 mm. long., the dorsum of carpels obtuse-angled, the sulci between the carpels deepest near the apex, where they extend a third to half way to the center of the fruit, sericeous-tomentose, canescent, hairs simple and forked, 0.5–1.2 mm. long, stellate 0.2 mm. long, the stipe 0–1.0 mm. long; dehiscence all along the ventral sutures and one-fourth the way along the dorsal sutures, also partly septicidal; seeds winged, the body 2–2.5 mm. long, 1.4–1.5 mm. wide, the wing 2.6–3.5 mm. high, extending 1.8 mm. beyond the body, 1.7–2.2 mm. wide just above the body, adaxial edge straight, abaxial edge convex.

Flowering specimens collected August to October; fruiting ones in September and October.

TYPE LOCALITY: Viti Levu, Fiji Islands, type cited below.

DISTRIBUTION: Viti Levu, Fiji Islands, in hillside and grassland thickets, usually in the sun, at 550–800 meters elevation.

FIJI ISLANDS: VITI LEVU: MBA (formerly Tholo North): Slopes of the escarpment N. of Nandarivatu, *A. C. Smith* 6040 (L, US, type). NANDRONGA AND NAVOSA: N. portion of Rairaimatuka Plateau, *A. C. Smith* 5588 (L, S, US). Mt. Evans Range, *Greenwood* 1229 (US), 1239 (US).

This species is closest to *M. degeneriana*. The lower surface of the leaf of the latter is subglabrous, that of *M. mollipila* is persistently

tomentulose. The capsule of *M. mollipila* is shorter than that of *M. degeneriana*, and broader than long; capsule of *M. degeneriana* is longer than broad.

8. Melochia roseiflora A. C. Sm. Journ. Arn. Arb. 31:331. 1950.

A shrub or tree 1–8 meters high, the young stems and petioles tomentulose, hairs brownish, stellate, 0.05–0.5 mm. long, average 0.2 mm., the internodes 0.3–7.0 cm. long; stipules 2.5–5.5 mm. long, 1.0–1.5 mm. wide, deltoid, acute, the abaxial surface tomentulose-hirsute, hairs stellate, 0.1–0.3 mm. long; petiole short, 0.3–1.5 cm. long.

Lamina 3.7–9.0 cm. long, 2.2–6.2 cm. wide, broadly ovate to lanceolate-ovate, the base usually rounded, sometimes cuneate, the apex acute to somewhat rounded, the upper surface somewhat shiny and rather dark green, subglabrous, hairs on the veins few, scattered, stellate, 0.1–0.2 mm. long, the lower surface lighter green, hairs on the veins scattered, stellate, 0.1–0.4 mm. long, the margin irregularly and rather shallowly crenate or crenate-serrate, crenations or serrations 1.2–5.5 mm. wide, 0.3–1.0 mm. high, 6–8 pairs of primary veins, 1 or 2 are basal, the second much stronger than the first.

Inflorescences fairly compact, 4–6.5 cm. long, in the axils of the upper 2 or 3 leaves, corymbiform, the flowers few to moderate in number, the ultimate divisions umbellate, the umbels 2- or 3-flowered, the peduncle 2.3–3.2 cm. long, with a primary branch 0.6–1.4 cm. long, and sometimes a secondary one to 0.5 cm. long, the pedicels deep pink, 1.5–3.0 mm. long in flower, to 5 mm. long in fruit; bracts 1.0–3.1 mm. long, 0.5–0.7 mm. wide, deltoid to lanceolate, acute, tomentulose-hirsute, hairs stellate, 0.1–0.2 mm. long.

Calyx deep pink, 4.5–5.0 mm. long, 6.0–6.5 mm. wide, tomentulose, hairs stellate, 0.05–0.2 mm. long, also a few glandular, 0.1–0.4 mm. long on the young calyx, the teeth 2.2–2.5 mm. long, 2.5–2.8 mm. wide, deltoid, acute to acuminate, the sides rounded, the sinus acute; petals bright pink, slightly paler than the calyx, 6.5–7.9 mm. long, 2.2–2.9 mm. wide, elliptic to slightly obovate, attached to the stamens for 1.5–1.7 mm., the claw 1.5–2.0 mm. long.

Longistylous form. Stamens 4.7–5.0 mm. long, the filaments free for 0.5 mm., the anthers yellow, 1.5–2.0 mm. long, 1.1–1.3 mm. wide, oblong, emarginate nearly to the middle from both ends; pistil 7.8–8.3 mm. long, the styles rich pink, filiform, papillose for 1–1.2 mm., free for 5.0–5.2 mm., united for 0.5–0.7 mm., proximal half tomentose, the ovary globular-ovoid to elliptic, densely tomentose, hairs 0.7–1.0 mm. long, the carpels sometimes 6, stipe none.

Brevistylous form. Stamens 8.1 mm. long, the filaments nearly white, free for 4.5 mm., the anthers 1.7–1.8 mm. long, 0.7–0.9 mm. wide;

pistil 4.8 mm. long, the styles recurved, 2 mm. long, filiform, free to the ovary, the ovary ovoid, densely sericeous, hairs 1 mm. long, the carpels sometimes 7.

Fruit 7.0–7.7 mm. long, of which the arista is 0.5 mm. long, 6.0–6.3 mm. wide, globular-ovoid, the dorsum of carpels obtuse-angled, the sulci between the carpels shallow, except in the distal half, where they extend a third of way to the center of the fruit, tomentose, hairs simple, forked and stellate, 0.3–1.2 mm. long, the stellate ones also 0.1 mm. long, stipe none; dehiscence all along the ventral sutures and a fourth to half way along the dorsal sutures, also partly septicidal; seeds brown, winged, the body 2.0–2.5 mm. long, 1.3–1.7 mm. wide, the wing 1.3–1.7 mm. high, 1.0–1.5 mm. wide, obliquely deltoid, apex acute or rounded.

Flowering specimens collected in April and May; fruiting ones in May.

TYPE LOCALITY: Viti Levu, Fiji Islands, isotypes cited below.

DISTRIBUTION: Viti Levu, Fiji Islands, in grassland-forest transition and in dense ridge forest and thickets, at 700–1,195 meters elevation.

FIJI ISLANDS: VITI LEVU: MBA: Northern portion of Mt. Evans Range, between Mt. Vatuyanitu and Mt. Natondra, *A. C. Smith* 4361 (L, US, isotypes). Summit of Mt. Koroyanitu, high point of Mt. Evans Range, *A. C. Smith* 4236 (L, S, US). Mt. Evans, *Greenwood* 316 (K).

This species appears to be closest to *M. degeneriana* and *M. mollipila*. The latter two have yellow flowers, those of *M. roseiflora* are bright pink. The petioles of *M. roseiflora* are usually shorter.

9. Melochia grayana A. C. Sm. Journ. Arn. Arb. 31:309. 1950.

Melochia vitiensis var. *β* A. Gray, Bot. U.S. Expl. Exped. 1:193. 1854.

A branched shrub 1.5–2 meters high, the young stems and petioles minutely tomentulose and cinereous or hairs scattered, stellate, forked, and simple, 0.05–0.3 mm. long, the internodes 0.2–3.2 cm. long; stipules 3.6–6.0 mm. long, 0.9–1.6 mm. wide, deltoid to lanceolate, acute to acuminate, subglabrous or ciliate, hairs few, simple, 0.1–0.3 mm. long; petiole 0.5–2.4 cm. long.

Lamina subcoriaceous, 3.1–7.3 (–9.0) cm. long, 1.1–2.4 (–4.5) cm. wide, lanceolate to elliptic, the base cuneate to narrowly rounded, the apex acute, the upper surface glabrous, the lower surface with few, scattered, simple, forked and stellate hairs 0.1–0.3 mm. long on the veins, the margin irregularly and shallowly serrate to crenate-serrate, serrations 1.3–5.7 mm. wide, 0.4–1.2 mm. high, 5–8 pairs of primary veins, 1 is basal.

Inflorescences loose, 5–10.5 cm. long, in axils of upper 3–5 leaves, corymbiform to subpaniculate, the flower number usually few, sometimes moderate, the ultimate divisions umbellate, the umbels 2–4-flowered, the peduncle 2–3.5 cm. long, with a primary branch 0.7–2.4

cm. long, sometimes a secondary one to 1.0 cm. long and a tertiary one to 1.6 cm. long, the pedicels 1–3.5 mm. long; bracts soon deciduous, 1.2–2.0 mm. long, 0.1–0.8 mm. wide, lanceolate to linear, tomentulose and ciliate, hairs stellate and forked, 0.1–0.2 mm. long.

Calyx orange-tinged to bright red, 5.5–6.7 mm. long, 4.0–5.5 mm. wide, tomentulose, hairs stellate and forked, usually 0.05–0.2, rarely to 0.5 mm. long, the teeth 2.2–3.2 mm. long, 1.5–2.5 mm. wide, deltoid, acute to acuminate, the sinus acute; petals yellow, 5–9 mm. long, 1.6–3.0 mm. wide, elliptic, suboval or oblong, the apex rounded, the base acute, attached to the stamens for 2.6–3.0 mm., the claw 1–2 mm. long.

Longistylous form. Stamens yellow, 4.5–5.2 mm. long, the filaments free for 1–2 mm., the anthers 1.7 mm. long, 1.1–1.2 mm. wide, oblong, deeply emarginate at both ends, sacs separate at the apex, pistil 5.7–7.1 mm. long, the styles slightly clavate, papillose for 0.8–1.0 mm., 2.9–4.5 mm. long, free to the ovary, the ovary narrowly ovoid, densely tomentose-sericeous, the carpels sometimes 7–8, stipe none.

Brevistylous form not seen.

Fruit. Only parasitized fruit seen.

Flowering specimens collected in October and November; fruiting ones in October.

TYPE LOCALITY: Vanua Levu, Fiji Islands, isotype cited below.

DISTRIBUTION: Vanua Levu, Fiji Islands, in forest, at 60–590 meters elevation.

FIJI ISLANDS: *Horne* 635 (GH) ?*M. grayana*, early bud stage. VANUA LEVU: MATHUATA: Summit ridge of Mt. Numbuiloa, E. of Lambasa, *A. C. Smith* 6525 (US, isotype). Muthuata, U.S. Expl. Exped. under Capt. Wilkes (US 13126, type of *M. vitiensis* var. *β*). Labasa, Macuata Coast, *Greenwood* 620A (K). Mt. Labasa, *Greenwood* 620 (K).

This species can be distinguished from the other species in the section *Visenia* by its lanceolate or elliptic leaves; the other species have at least some ovate leaves, and they are usually considerably broader.

10. Melochia compacta Hochr. Ann. Conserv. Jard. Bot. Genève 21:429. 1920.

A shrub or small tree 1–6 meters high, the young stems and petioles tomentulose, hairs tan, stellate, and usually also forked and simple, 0.1–0.6 mm. long, the internodes 0.5–1.0 (–4.5) cm. long; stipules 3.3–8.0 (–9.0) mm. long, 1.7–4.1 (–5.0) mm. wide, lanceolate to ovate, acuminate, hirsute or tomentulose, hairs forked and simple, 0.1–0.5 mm. long; petiole 1–6.5 (–13) cm. long.

Lamina 6.2–16 (–28) cm. long, 4.8–12.5 (–24) cm. wide, ovate, the base rounded to cordate, the apex acute, often densely tan-canescent when young, both surfaces of older leaves glabrescent, hairs scattered,

stellate and usually also forked and simple, 0.1–1.0 mm. long, the margin irregularly crenate-serrate, serrations 0.9–8.0 mm. wide, 0.3–1.7 mm. high, 8–10 pairs of primary veins, 2 or 3 are basal.

Inflorescences 3.5–20 cm. long, usually compact, flower number moderate to fairly abundant, in the axils of the upper 3–5 leaves, corymbiform, the ultimate divisions umbellate, the umbels about 5-flowered, the penduncle 2–16 cm. long, with a usually short primary branch 0.5–4.0 cm. long, sometimes a secondary one 0.3–1.5 cm. long, and a tertiary one 0.5–1.0 cm. long, the pedicels short, 0–3 mm. long; bracts rather broad, sometimes 2 united, 2–4.5 mm. long, 0.8–3.0 mm. wide, ovate to lanceolate, tomentulose or hirsute and ciliate, hairs simple, forked, and stellate, 0.1–0.9 mm. long.

Calyx 6–9 mm. long, 5.3–8.0 mm. wide, tomentulose and sericeous, hairs stellate and forked, 0.1–1.0 mm. long, the teeth 2.3–5.4 mm. long, 2–4 mm. wide, deltoid to ovate, acuminate or acute, the sinus acute; petals pink, red proximally and pink or white distally, rarely rose and yellow, or white, 6.3–15.5 mm. long, 2.3–7.5 mm. wide, obovate-cuneate, attached to the stamens for 1–2.5 mm., the claw 1.5–3.0 mm. long.

Longistylous form. Stamens 5–6 mm. long, the filaments united up to the anthers or free for 0.5 mm., the anthers 1.2–1.9 mm. long, 0.6–1.2 mm. wide, oblong, emarginate at both ends; pistil 5.2–9.0 mm. long, the styles filiform, slightly clavate, papillose for 0.8–2.0 mm., free for 2.9–6.0 mm., to the ovary, or united for 0.5 mm., the ovary ovoid or elliptical, densely sericeous, hairs simple and forked, 0.5–1.5 mm. long, stipe none.

Brevistylous form. Stamens 6.2 mm. long, the filaments free for 2–3 mm., the anthers 1.2–1.3 mm. long, 0.7 mm. wide; pistil 3.6 mm. long, the styles filiform, 2.0 mm. long, free to the ovary, the ovary densely sericeous, hairs simple and forked, 1–1.4 mm. long.

Fruit (4–) 5.2–9.0 (–10) mm. long, with an arista 0.5–2.0 mm. long, 4.2–6.5 mm. wide, globular-ovoid, the dorsum of carpels rounded, the sulci between the carpels shallow, extending one-fifth the way to the center of the fruit, tomentulose and sericeous, hairs simple, forked and stellate, 0.1–1.5 mm. long, the stipe 0–0.9 mm. long; dehiscence all along the ventral sutures and a third to half way along the dorsal sutures, partly septicidal; seeds wingless, 2.4–3.5 mm. long, 1.2–1.9 mm. wide.

Flowering specimens collected in March, April, and June to December; fruiting ones in March and June to December.

TYPE LOCALITY: Marianas Islands, probably Guam. The type was collected by Gaudichaud and is cited below.

DISTRIBUTION: Palau, Yap, and Marianas Islands, in forest or on cleared land, on coastal plain, on limestone, at 1–170 meters elevation.

227–051—67——4

CAROLINE ISLANDS: PALAU ISLANDS: Peleliu Island, SW. side, *Fosberg* 25983 (BISH, US). Urukthapel Island, E. end, around lighthouse on top of peak, *Fosberg* 32039 (BISH, US). YAP ISLANDS: YAP ISLAND: *Hallier* 547 (L). *Kanehira* 1121 (US). Low E. ridge of Mt. Matade, slopes just above Yap Town, *Fosberg* 25574 (BISH, US). RUMUNG: *Ross* Oct. 5, 1949 (US). TOMIL ISLAND: *Hosaka* 3293 (BISH, US). ULITHI ATOLL: Mogmog Island, *Knox* 829 (US); *Fosberg & Wong* 25471 (BISH, US). Potangeras Island, *Hosaka* 3237 (BISH, US).

MARIANAS ISLANDS: *Gaudichaud* 66 (G, type, US neg. 5415). GUAM: Oca Point, *Moore* 43 (US). Machanao Dist., *Bryan* 1197 (US). N. of NW. Field, *Steere* 1 (US). N. end of Harmon Field, *Fosberg* 39252 (BISH, US). Ritidian Point, *Fosberg* 25317 (BISH, US); *Hosaka* 3091 (BISH, US); *Anderson* 218 (BISH, US). Vicinity of Agaña, *Anderson* 174 (BISH, US). ROTA: Rota and vicinity, *Fosberg* 25068 (BISH, US). NW. coast of W. end of main part of island, between Rota and Tataacho Point, *Fosberg* 25017 (US). SAIPAN: W. of Lake Susupe, *Fosberg* 25264 (BISH, US).

This species is closest to *M. villosissima*. Differences are given under the description of the latter species.

11. Melochia villosissima (Presl) Merr. Philip. Journ. Sci. 15:543. 1919.
Riedlea villosissima Presl, Rel. Haenk. 2:146. 1835.
?*Melochia Lessoniana* K. Schum. ex Volkens, Eng. Bot. Jahrb. 31:468. 1902, nomen nudum.
Melochia hirsutissima Merr. Philip. Journ. Sci. 9:113. 1914.

Usually a shrub, sometimes a small tree, 0.7–7.6 meters high, the young stems and petioles densely fuscous-rufescent tomentose, hairs forked, simple, and stellate, 0.3–2.0 mm. long, the internodes 0.3–14 cm. long; stipules 2–5 (–9) mm. long, 1.0–2.5 (–7.0) mm. wide, lanceolate to ovate, acute, sericeous-tomentose and ciliate, hairs forked, stellate, and simple, 0.7–2.0 mm. long; petiole 1.1–14.5 cm. long.

Lamina 4.4–30 cm. long, 3.0–21.5 cm. wide, ovate, largest blades sometimes with a pair of lateral lobes 2 cm. high and 2 cm. wide, the base rounded to cordate, the apex acute, typically canescent and densely woolly on both surfaces, hairs forked and stellate (shorter ones), 0.2–1.2 mm. long, the margin irregularly crenate-serrate, serrations 1.1–3.2 mm. wide, 0.5–1.1 mm. high, 6–8 pairs of primary veins, 2 are basal.

Inflorescences usually compact, 4–14 cm. long, in axils of upper 4–6 leaves, corymbiform, flowers fragrant, number usually moderate, sometimes few or numerous, the peduncle thick, 2–3.5 mm. wide, 2.8–9.0 (–15.5) cm. long, usually with a short primary branch to 1.0 (–5.5) cm. long, rarely a secondary one 0.5 (–2.5) cm. long, rarely a tertiary one 0.5 (–3.0) cm. long, the pedicels usually very short, 1–2 (–4) mm. long; bracts 2–3.5 mm. long, 1.1–2.5 mm. wide, ovate, acute to rounded at the apex, hirsute and ciliate, hairs forked, stellate, and simple, 0.3–1.3 mm. long.

Calyx thick, 7.9–8.7 mm. long, 5.2–7.0 mm. wide, densely sericeous-tomentulose, hairs ferruginous, stellate and forked, 0.2–1.5 mm. long, the teeth 3.3–4.0 mm. long, 2.7–3.3 mm. wide, deltoid to ovate,

acute to slightly acuminate, the sinus acute; petals pink to red, sometimes fading distally, rarely magenta, relatively thick, 7.4–8.9 mm. long, 3–5 mm. wide, obovate, sometimes emarginate, attached to the staminal tube for 1–1.7 mm., the claw 1.5–2.0 mm. long.

Longistylous form. Stamens 5.2 mm. long, the filaments united up to the anthers, the staminal tube rose colored, the anthers 1.7–1.9 mm. long, 1.2–1.4 mm. wide, oblong, emarginate nearly to the middle from both ends; pistil 8.5 mm. long, the styles filiform, papillose for 1.5 mm., free to the ovary, 5.0 mm. long, the ovary ovoid, densely sericeous, hairs 0.9–1.8 mm. long, stipe none.

Brevistylous form. Stamens 5.8–6.1 mm. long, the filaments free for 3 mm., the anthers 1.8–1.9 mm. long, 0.7–0.9 mm. wide; pistil 5.3 mm. long (some development), the styles 2 mm. long, the ovary globular-ovoid, densely sericeous-tomentose, hairs to 1.7 mm. long.

Fruit (4–) 6.4–7.0 (–8.0) mm. long, of which 1–1.5 (–3) mm. is arista, 5.2–6.0 mm. wide, globular-ovoid, the dorsum of carpels obtuse-angled, the sulci between the carpels shallow, in the distal half of the fruit, extending a fifth to half way to its center, densely tomentose, hairs simple, forked, and stellate, 0.3–1.3 mm. long, the stipe 0–0.5 mm. long; dehiscence all along the ventral sutures and a fifth to half way along the dorsal sutures, also partly septicidal; seeds generally wingless, 3.0–3.5 mm. long, 1.5–2.0 mm. wide, trigonal, of 10 seeds examined only one had a faint indication of a wing, 0.3 mm. high and 1 mm. wide, the apex rounded.

Flowering and fruiting specimens collected throughout the year except in November, most commonly in June to September.

TYPE LOCALITY: Guam.

DISTRIBUTION: Caroline and Marianas Islands, usually in disturbed, open, shrubby areas previously cultivated, on soils or rocks of volcanic or limestone origin, at 1–360 meters elevation.

CAROLINE ISLANDS: Tjaperna plateau (?Kusaie), *Hallier* Aug. 27, 1903 (L). PALAU ISLANDS: Arukoron-sôgen, *Hosokawa* 7044 (A, US). BABELDAOB ISLAND: E. coast, hills between Melekiok and Lake Ngardok, *Fosberg* 32596 (BISH, US). NGARAKABESANG (ARAKABESAN) ISLAND: S. side of W. peninsula, *Fosberg* 32131 (BISH, US). GASPAN: *Hosokawa* 9641 (A). TRUK ISLANDS: MOEN ISLAND: E. end, *Hosaka* 2795 (BISH, US); Slopes of Mt. Tonaachau (Toladjau), *Fosberg* 24431 (BISH, US). DUBLON ISLAND: *Fosberg* 24536 (BISH, US). SENYAVIN ISLANDS: PONAPE: Matalanim, *Hosaka* 3548 (BISH, US). KUSAIE: *Kanehira* 1343 (US). Lelehafen's Königsland, *Hallier* Sept. 3, 1903 (L). Lowest slopes and foot of S. side of Mt. Matanta (Buache) N. of head of Lela Harbor, *Fosberg* 26570 (BISH, US). LELU ISLAND: *Clarke* Ku–78 (US).

MARIANAS ISLANDS: GUAM: *McGregor* 456 (L, US, isotypes of *M. hirsutissima*). *Nelson* 1 (US), 353 (US). Facpi Point, approach to Mt. Lamlam, *Necker* 374 (US). Near Telefofo (?Talofofo) River, *Rodin* 683 (US). Agat, Achugao, *Hosaka* 3192 (BISH, US). Mt. Tenjo and Mt. Reconnaisance area, *Moore* 217 (US). S. of Asan Point and Piti, *Anderson* 73 (BISH, US). Lower

Fonte River, W. of Agaña, *Fosberg* 31238 (BISH, US). Chalandao Mt. 1 km. SE. of Jumujong Manglo Mt., *Fosberg* 35379 (BISH, US). Anao (?Anae), above cliffs, *Fosberg* 38639 (BISH, US). Com.-Marianas Fuel Storage Area, *Fosberg* 35213 (BISH, US). Mataguac, *Moran* 4449 (US). ROTA: *Necker* R52 (US). *Kanehira* 1762 (US). *Hosokawa* 7556 (A, US). Airstrip, N. of Shimapaaru, *Fosberg* 25158 (BISH, US). SAIPAN: Oleai, *Fosberg* 31283 (BISH, US). Raishingan, *Hosokawa* 8028 (US). PAGAN: *Anderson* 501 (BISH, US). AGRIHAN (AGRIGAN): Trail around S. side of island on coastal strip, a narrow shelf, *Fosberg* 31567 (BISH, US).

This species is closest to *M. compacta*. The leaves of the latter are glabrescent, those of *M. villosissima* are persistently fairly densely hairy. The hairs of the young stems of *M. villosissima* are twice as long as those of *M. compacta*.

Section II. *Mougeotia* Griseb. Fl. Brit. W. Ind. 94. 1859

Section *Anamorpha* Triana & Planch. Prodr. Flo. Novogran. 215. 1862.

Perennial, rarely annual, herbs to shrubs, rarely a small tree, 0.1–5.0 meters high, the taproot not thicker than the base of the stem or to 2.5 times thicker and 0.4–2.2 cm. wide, the young stems tomentulose, hirsute or pilose, sometimes canescent, hairs sometimes tan, golden or ferruginous, simple, stellate, forked, or glandular, 0.1–4.0 mm. long, internodes 0.4–11.0 cm. long; stipules 1.5–10.3 mm. long, 0.2–4.0 (–5.0) mm. wide, usually deltoid-acuminate or deltoid-acute or lanceolate, usually ciliate, and hirsute, sericeous or tomentulose, hairs simple, stellate or forked, rarely also glandular, 0.1–3.5 mm. long; petiole 0.1–6.7 (–8.0) cm. long.

Lamina 0.8–14.0 (–22) cm. long, 0.2–8. 8 (–10.5) cm. wide, usually ovate or lanceolate, sometimes oblong-ovate or nearly orbicular, the base rounded to cordate, sometimes truncate, the apex usually acute or acuminate, sometimes rounded, both surfaces glabrate, tomentulose, sericeous or velutinous, hairs simple, forked, or stellate, rarely also glandular, 0.1–4.0 mm. long, the margin irregularly crenate-serrate, serrations 0.5–8.5 mm. wide, 0.3–3.6 mm. high, 5–14 (–15) pairs of primary veins, usually 2 are basal.

Inflorescences axillary, terminal, or both, 0.6–21.0 (–31) cm. long, spicate, subcapitate, paniculate, umbellate, or corymbiform, the flowers sometimes very fragrant, the peduncle 0–8.5 cm. long, rarely a primary branch 0.4–3.5 cm. long and a secondary one 0–1.5 cm. long, the pedicel 0–9.3 mm. long; bracts 0.5–9.5 mm. long, 0.1–3.9 (–4.8) mm. wide, usually narrower than the stipules, sometimes several immediately subtending each flower and sometimes 2 or 3 united part way, pubescence similar to that of the stipules.

Calyx at anthesis 3.0–7.8 (–8.5) mm. long, 2.4–6.5 mm. wide, sometimes accrescent, becoming up to 12.3 mm. long, 12.0 mm. wide,

tomentulose, hirsute or sericeous, sometimes ciliate, hairs simple, stellate, glandular or forked, 0.1–1.3 (–4.0) mm. long, the teeth 1.3–5.3 (–6.5) mm. long, 0.5–2.8 (–5.5) mm. wide, the sinus usually acute, sometimes narrowly rounded; petals usually yellow to orange, or white, sometimes pink, reddish, white with red veins or purple, 3.7–12.0 mm. long, 1.4–5.0 mm. wide, usually obovate or oblanceolate, cuneate, free of the staminal tube or attached to it for 0.3–1.5 (–2.7) mm., the claw 0–1.5 (–4.0) mm. long, rarely a few hairs just above the claw; anther 0.7–2.1 mm. long, 0.4–1.1 mm. wide, oblong, emarginate at both ends, usually to the middle from the apex, staminodes rarely present, 0.1–0.4 mm. long.

Longistylous form. Stamens 2.4–5.9 mm. long, the filaments united up to the anthers, but separate for 0.5–1.0 mm. in *M. ulmifolia*, rarely tufts of hair 0.4–1.3 mm. long present at the base of the staminal tube, alternate with the filaments, hairs 0.1–0.2 mm. long; pistil 2.6–8.8 (–12) mm. long, the styles free for 1.2–5.3 mm., usually to the ovary, sometimes united for 0.3–4.0 mm., papillose at the apex for 0.5–1.2 mm.

Brevistylous form. Stamens 2.8–8.2 mm. long, the filaments free for 0.5–5.0 mm.; pistil 2.3–6.0 mm. long, the styles free for 1.1–2.5 mm., usually to the ovary, sometimes united for 0.2–0.7 mm., papillose for 0.3–0.7 mm. at the apex.

Fruit 2.5–7.5 mm. long, 2.9–6.5 mm. wide, globular, pentagonal, the carpels usually obtuse at the base and carinate above the middle, the sulci usually shallow, extending one-fifth to one-third, rarely half, the way to the center of the fruit, usually tomentulose or hirsute, hairs usually stellate, forked, and simple, sometimes also glandular, 0.1–1.0 mm. long, the stipe 0–1.0 mm. long; dehiscence usually septicidal into cocci, or sometimes along the entire ventral suture and a third to half way along the dorsal suture and slightly septicidal or tardily septicidal and the fruit falling apart; seeds 1.5–3.0 mm. long, 0.9–2.0 mm. wide, rarely the chalazal end loosened, membranous, and almost winglike for 0.1–0.3 mm., usually 1 per cell but often 2.

LECTOTYPE: *Melochia pilosa* (Mill.) Fawc. & Rendle.

DISTRIBUTION: Mexico, West Indies, Central America, and South America to Argentina, in thickets, llanos, fields, savanna and woods, at 0–3,150 meters elevation.

12. **Melochia pilosa** (Mill.) Fawc. & Rendle, Fl. Jamaica 5:164. 1926.
Sida pilosa Mill. Gard. Dict. ed. 8. 1768.
Melochia venosa Sw. Prodr. Veg. Ind. Occ. 97. 1788.
Mougeotia polystachya H. B. K. Nov. Gen. & Sp. 5:328, *pl. 483.* 1823.
Riedleia polystachya (H. B. K.) DC. Prodr. 1:490. 1824.
Riedleia Jamaicensis DC. Prodr. 1:492. 1824.

Melochia Jamaicensis Balb. ex DC. Prodr. 1:492. 1824.
Riedleia venosa (Sw.) DC. Prodr. 1:492. 1824.
Melochia sericea St.-Hil. Fl. Bras. Mer. 1:160. 1825.
Melochia ulmarioides St.-Hil. Fl. Bras. Mer. 1:159. 1825.
Visenia polystachya (H. B. K.) Spreng. Syst. 3:30. 1826.
Visenia venosa (Sw.) Spreng. Syst. 3:30. 1826.
Visenia sericea (St.-Hil.) Spreng. Syst. 4:Cur. Post. 248. 1827.
Visenia Ulmariae Spreng. Syst. 4:Cur. Post. 248. 1827.
Riedleia virgultosa Macfad. Fl. Jamaica 1:104. 1837.
Riedleia interrupta Schlecht. Linnaea 11:375. 1837.
Riedleia sericea (St.-Hil.) Steud. Nom. II, 2:460. 1841.
Riedleia Ulmariae (Spreng.) Steud. Nom. II, 2:460. 1841.
Melochia gracilis St.-Hil. & Naud. Ann. Sci. Nat. II, 18:35. 1842.
Melochia nitidula St.-Hil. & Naud. Ann. Sci. Nat. II, 18:35. 1842.
Melochia polystachya (H. B. K.) Triana & Planch. Ann. Sci. Nat. IV, 17:341. 1862.
Melochia interrupta (Schlecht.) Hemsl. Biol. Centr. Amer. Bot. 1:131. 1879.
Riedleia argentea Poepp. ex Schum. *in* Mart. Fl. Bras. 12(3):37. 1886, in synonymy.
Melochia betonicaefolia Ruiz & Pavon ex Schum. *in* Mart. Fl. Bras. 12(3):37. 1886.
Melochia paniculata Willd. ex Schum. *in* Mart. Fl. Bras. 12(3):37. 1886.
Melochia venosa Sw. var. *typica* Schum. *in* Mart. Fl. Bras. 12(3):37. 1886.
Melochia venosa Sw. var. *polystachya* (H. B. K.) Schum. *in* Mart. Fl. Bras. 12(3):37. 1886.
Melochia venosa Sw. var. *betonicifolia* Schum. *in* Mart. Fl. Bras. 12(3):37. 1886.
Melochia venosa Sw. var. *sericea* (St.-Hil.) Schum. *in* Mart. Fl. Bras. 12(3):38. 1886.
Melochia venosa Sw. var. *Widgrenii* Schum. *in* Mart. Fl. Bras. 12(3):38. 1886.
Melochia "nervosa" (=venosa Sw.) *β polystachya* (H. B. K.) Schum. var. *flava* O. Ktze. Rev. Gen. 3(2):25. 1898.
Melochia venosa Sw. var. *squarrosa* Schum. & Hassl. Bull. Herb. Boiss. II, 4:71, in 1903 for 1904.

An erect herb or suffrutex, sometimes frutex, 0.4–3.0 (–4.0) meters high, simple or branched, the branches slender, to 15 cm. long, sometimes 2 or more shoots from near the base, the root thickened, to 2.5 times the diameter of the base of the stem, 0.8–1.2 cm. wide, woody; young stems sometimes hollow, hirsute, pilose or tomentose, sometimes woolly, hairs tan or golden, sometimes ferruginous, mostly simple, sometimes also glandular and a few forked or stellate, 0.1–2.2 mm. long, internodes 0.8–8.0 cm. long; stipules deciduous, (3–) 4–10 mm. long, 0.7–4.0 mm. wide, deltoid-acuminate, ovate-acute, or lanceolate, sometimes slightly oblique, sericeous, ciliate, hairs simple, 0.2–1.5 mm. long; petiole 0.2–2.7 (–5.0) cm. long, pubescence similar to that of the young stems.

Lamina 2.2–9.5 (–11) cm. long, 0.9–7.5 cm. wide, ovate, oblong-ovate, ovate-lanceolate, lanceolate, or subelliptic, the base rounded to subcordate, the apex acute to somewhat rounded, leaves im-

mediately below the inflorescence reduced, the upper surface usually green, sericeous, hirsute or puberulous, sometimes glabrescent, sometimes scabrous or woolly to the touch, hairs simple, sometimes a few forked or stellate, 0.2–1.0 mm. long, the lower surface green, or covered with brownish, golden or ferruginous hairs, sericeous or pilose on the veins, hairs simple, to 1.3 mm. long, sometimes densely tomentulose between the veins with hairs erect, stellate, forked, and simple, rarely also glandular, 0.2–0.7 mm. long, velvety or woolly to the touch, sometimes glabrescent, the margin irregularly crenate-serrate, serrations 0.6–4.8 mm. wide, 0.3–2.7 mm. high, primary veins numerous, (7–) 8–11 (–13) pairs, 2 or 3 are basal, more or less parallel, straightish and ascending at a rather acute angle (about 40°), impressed above, prominent beneath.

Inflorescences principally terminal, extending (2–) 10–20 (–31) cm. beyond the first leaf, at 3–11 nodes, paniculate, contracted or open, sometimes spicate, the flowers tending to be more numerous on the upper side of the brachlets, in subcapitate umbels of (1–) 3–12 flowers, the branchlets 1.5–3.5 cm. long, usually also axillary, 1–11.8 cm. long, in the axils of 1–5 or more reduced leaves, at 1–3 nodes, the peduncle 0–0.3 cm. long, the pedicel usually short, 1–3 (–5) mm. long; bracts usually separate, rarely 2 or 3 united at the base, 1.5–5.0 mm. long, 0.2–2.1 mm. wide, deltoid-acute to deltoid-acuminate, ovate, lanceolate or linear, ciliate, sericeous, hairs simple, 0.1–1.0 mm. long.

Calyx (4.0–) 4.6–7.5 mm. long, (2.5–) 2.9–5.3 mm. wide, not accrescent, external surface hirsute, sericeous, or tomentulose, hairs simple, sometimes also glandular, stellate or forked, 0.1–1.0 mm. long, the internal surface densely puberulous at the apex, the teeth 2.5–4.7 mm. long, 0.9–2.2 mm. wide, deltoid-acuminate or deltoid-acute, the sinus acute or narrowly rounded; petals usually yellow, sometimes orange, 5.9–10.5 mm. long, 2.0–4.5 mm. wide, obovate to oblanceolate, sometimes cuneate, the claw 1–2 mm. long, attached to the staminal tube for 0.5–1.0 mm.

Longistylous form. Stamens 3.4–5.3 mm. long, the filaments united up to the anthers, the anther 0.9–1.5 mm. long, 0.5–0.7 mm. wide, oblong, emarginate at both ends, nearly to the middle from the apex; pistil 4.6–8.3 mm. long, the styles 2.6–5.0 mm. long, free to the ovary or united for 0.5 mm., stigmatic for 0.5–1.0 mm., the ovary oblong, ellipsoid, ovoid or globular, densely hirsute-sericeous at the apex, less so below, hairs 0.2–1.5 mm. long, stipe none.

Brevistylous form. Stamens (5.1–) 6.3–7.5 mm. long, the filaments free for 2.6–4.2 mm., glabrous, the anther 1.1–1.3 mm. long, 0.6–0.8 mm. wide, shape same as that above, sometimes very small staminodal teeth present; pistil (3.3–) 3.7–4.7 mm. long, the styles (1.1–) 1.7–2.2 mm. long, free to the ovary or united for 0.2–0.5 mm.,

stigmatic for 0.3–0.5 mm., the ovary globular-ovoid, densely hirsute-sericeous, hairs simple, 0.2–1.0 mm. long.

Fruit globular or suboblong, obtusely pentagonal, (3.7–) 4.2–6.0 mm. long, (3–) 4.2–5.0 mm. wide, usually slightly longer than wide, the rostrum 0.3 mm. long, hirsute-tomentulose, hairs simple, 0.3–1.1 mm. long, sometimes also forked and stellate, rarely glandular, 0.1–0.2 mm. long, the sulci between the carpels very shallow, extending a fifth to a fourth the way to the center of the fruit, the base sometimes narrowed into a stipe 0.5 mm. long; dehiscence all along the ventral suture and a third to half way along the dorsal suture, eventually also septicidal, the fruit falling apart; seeds 1.6–2.7 mm. long, 1.1–1.6 mm. wide, dark brown, 1 or 2 per cell.

Flowering and fruiting specimens collected throughout the year.

TYPE LOCALITY: Jamaica. Miller's type is in the herbarium of the British Museum.

DISTRIBUTION: Vera Cruz, Mexico, Jamaica, Venezuela, Colombia, southern and western Brazil, Ecuador, Peru, Bolivia, Paraguay and northern Argentina, in campo and thickets, usually in dry, open habitats, in savanna, on hillsides, in rocky, calcareous soil, at 224–2,000 meters elevation, usually above 500 meters.

MEXICO: VERA CRUZ: Hacienda de la Laguna, *Schiede* s.n. (P, isotype of *Riedleia interrupta* Schlecht.). F neg. 35381 ex P of type of *Riedleia interrupta* Schlecht. (US). ?VERA CRUZ: Pacho (?Pacho Viejo), *Liebmann* 11874 (US).

JAMAICA: *Swartz* s.n. (S, type of *Melochia venosa* Sw., also US neg. 5606). *Balbis* s.n. (S). Constitution Hill, *Harris* 6815 (US), 9026 (US). Along the road to Newcastle, *Rishbeth* s.n. (IJ).

VENEZUELA: *Vogl* 334 (S). MIRANDA: San Blas?, *Gines* 4414 (US). FEDERAL DISTRICT: Caracas and vicinity, *Pittier* 6151 (US); *Curran & Haman* 1063 (US); *Martin*? (S). Road from Caracas to La Guayra, *Pittier* 5898 (US), 9557 (US). Lower Catuche wood above Caracas, *Pittier* 7027 (US). Lower Cotiza near Caracas, *Pittier* 7888 (MICH, US). Rio Catuche, *Eggers* 13062 or 13162, July 9, 1891 (L). ARAGUA: Colonia Tovar, La Victoria, *Fendler* 111 (GH), 1929 (GH). COJEDES: San Carlos, *Velez* 2753 (US). MÉRIDA: Tabay, *Gehriger* 444 (US).

COLOMBIA: *Triana* s.n. (W). MAGDALENA: Sierra Nevada de Santa Marta, *Barkley & Araque M.* 38 (US). Between Pueblo Viejo and San Miguel, *Seifriz* 354 (US). Santa Marta, *H. H. Smith* 471 (L, S, US). NORTE DE SANTANDER: Ocaña, *Schlim* 73 (P). SANTANDER: Upper Rio Lebrija valley, NW. of Bucaramanga, *Killip & Smith* 16307 (US). CUNDINAMARCA: Sasaima, *Bro. A. Marie* 20E (US). TOLIMA: Honda, *Humboldt & Bonpland* 1803 (P, isotype of *Mougeotia polystachya* H. B. K., also US neg. 5669). Mariquita, *Pennell* 3627 (US). HUILA: E. of Neiva, *Rusby & Pennell* 496 (US). San Antonio Fortalecillas, *Fosberg* 19837 (US). ANTIOQUIA: Bello, *Archer* 138 (US). CALDAS: Anserma, *Pennell* 10637 (US). Supia, *Pennell* 10696 (US). VALLE DEL CAUCA: Palmira, *Pennell & Killip* 6033 (US). Puerto Caldas, *Killip & Hazen* 11033 (US). CAUCA: Rio Patia, *von Sneidern* 2401 (S, US).

ECUADOR: "Yapio cerca Quilichao," *Jameson* s.n. (US).

PERU: *Mathews* 3307 (S). Vitoc and Chacahuassi, F neg. 9609 of *Ruiz*

s.n. ex B, presumably of type of *Melochia venosa* Sw. var. *betonicifolia* Schum. (US). CAJAMARCA: Jaen, *Weberbauer* 6200 (US). Valley of Tabaconas River, *Weberbauer* 6244 (US). SAN MARTÍN: Tarapoto, *Ferreyra* 5104 (US). Alto Rio Huallaga, *Ll. Williams* 6685 (US), 5802 (S). LORETO: Near Tarapoto, *Ule* 6436 (L). HUÁNUCO: Cuchero, *Poeppig* addenda 71 (W), 1269, in part (W). CUSCO: Lares Valley between Calca and Pasto Grande, *Weberbauer* 7932 (S, US).

BOLIVIA: Chiquiacá, *Fiebrig* 2722 (L). Florida and Palissa, *Herzog* 1294 (L, S). Ixiamas, *Cardenas* 1916 (MICH). Guanai, *Rusby* 1846 (MICH). Yungas and vicinity, *Rusby* 1847 (MICH); *Bang* 517 (MICH, US), 2810 (MICH, S, US). NORTH YUNGAS: Milluguaya, *Buchtien* 789 (S), 6021 (S). BENI: Trinidad-Missiones Guarayos, *Werdermann* 2504 (S). SANTA CRUZ: SARA: Buena Vista, *Steinbach* 7413 (S).

BRAZIL: *Pohl* 560 or 160 (W). MINAS GERAIS: Near São Antonio de Rio to Cima not far from Villa Rica (=Ouro Preto), *St.-Hilaire* 2295 (P, isotype of *Melochia sericea* St.-Hil., also US neg. 5673). Caldas, *Regnell* I 20 (R, S, US), I 20a (US); *Widgren* 245 (GH, S); *Lindberg* 285a (S), 284a (S). Corinto, Fazenda do Diamante, *Mexia* 5549 (GH, MICH, R, S, US). Ituiutaba, *Macedo* 4159 (US). Itabira do Campo, *Schwacke* s.n. (R). Belo Horizonte, Colonia Bias Fortes (Jardim Bot. Bel. Horiz. 5356). Belo Horizonte, *Barreto* 7862 (R), 10380 (R). Caxambu near das Aguas, *Glaziou* 15848 (R). Mantiqueira pelo vale do rio Verde até Três Corações, *de Saldanha* 8724 (R). Lagoa Santa, *Warming* s.n. (S). Between Sitio and Dr. Sa Fortes, Serra Mantiquerra, *Chase* 8675 (GH). SANTA LUZIA: Venda Nova, *L. O. Williams & Assis* 6511 (US). CAMPINA VERDE: Manga, *Macedo* 362 (US). GOIÁS: Near the city of Goiás, *Burchell* 6993 (K). São Domingos, *Gardner* 4105 (GH). Corallinho, *Pohl* 1310 (W). Caretão, *Pohl* (W). JATAI: Queixada, *Macedo* 1549 (US). MATO GROSSO: Coxipo da Ponte, *Hoehne* 3026 (726)(R). Maribondo St. Laurenço, *Hoehne* 2995 (721)(R). Tapirapoan, *Hoehne* 1511 (R). Porto Esperidião, Jaurú, *Hoehne* 704 (327)(R). Casa da Pedra, *Armond* (R 78143). Coxipo Mirim near Cuyabá, *Malme* s.n. (S). SÃO PAULO: *Burchell* 5618 (K). Itú, *Riedel* 1993 (W). Near Mogyguassú *Mosén* 1127 (S). PARANÁ: Jaguariahyva, *Dusén* 16172 (S, US); *Jonsson* 353a (S). Restinga Secca, *Dusén*, 4238 B(R). Seugés-Fabio Rego, *Dusén* 10979 (S). Capão Grande, *Dusén* 9167 (S). Morungava, *Dusén* 17384 (S). Itaperussú, *Dusén* 13855 (S). TIBAGI: Fda. Monte Alegre, Harmonia, *Hatschbach* 2872 (US), 2972 (US). CAMPO MOURÃO: Campo Mourão, *Hatschbach* 8770 (US). SANTA CATARINA: Rio Capinzal, *Dusén* 17851 (GH, S). CURITIBANOS: Butia campo, 19 km. E. of Lebon Regis, *L. B. Smith & Klein* 11052 (US). Curitibanos, *Miller* 83 (R). CAÇADOR: 31 km. W. of Caçador, *L. B. Smith & Klein* 10921 (US). CAMPOS NOVOS: 33 km. SE. of Campos Novos, *L. B. Smith & Klein* 11205 (US). Ile Sainte Catherine *Gaudichaud* s.n. (P). RIO GRANDE DO SUL: Santa Maria, Allenoa *Vidal* (R 78201, US); ?*Vida* (R); *Malme* 1236 (S). São Leopoldo, *Leite* 2518 (A); *Rambo* (PACA 1161), (PACA 1289); *Theissen* 398 (PACA), 582 (PACA), (PACA 25115); *Ritter* (PACA 35405). Sapucaia near São Leopoldo, *Rambo* (PACA 38174), (PACA 40768), (PACA 44277). Cristo Rei near São Leopoldo, *Rambo* (PACA 46206). Vicinity of TUPANCIRETÃ: Jarí, *Rambo* (PACA 9142), (PACA 9485). Ijusinho, *Rambo* (PACA 9989). At Ivaí River, *Rambo* (PACA 9474). Vicinity of SÃO LUIZ: Caaró, *Rambo* (PACA 53454). Cerro Largo, *Sehnem* (PACA 48091). Lagoa Vermelha and vicinity, *Friderichs* (PACA 11134), (PACA 11859). Passo do Socorro, *Rambo* (PACA 51506). Nonoai near Uruguay River, *Rambo* (PACA 28272). Cachoeira, *Malme* 988 (S). Santo Angelo, *Rambo* (PACA 53001). Kappesberg near Montenegro, *Sehnem* (PACA 48376). São Borja, *Rambo* (PACA

3029). Palmeira, *Rambo* (PACA 50011). Neu-Württemberg (Panambi), *Bornmueller* 433 (GH). Near an abrupt descent, called Salto, in the swifty flowing Uruguay River, *St.-Hilaire* 2526 (P, isotype of *Melochia ulmarioides* St.-Hil., also F neg. 35387 ex P, type of *Melochia ulmarioides* St.-Hil. (US).

URUGUAY: Cuñapirú (Brazilian frontier), *Rambo* (PACA 4024).

PARAGUAY: San Luis between Rio Apa and Rio Aquidaban, *Fiebrig* 4412 (GH, K, L). Upper part of Rio Apa, *Hassler* 8058 (GH, S, isotypes of *Melochia venosa* Sw. var. *squarrosa* Schum. & Hassl.). Near Bellavista (Rio Apa), *Hassler* 8184a (GH, S). Villarrica, *Jorgensen* 3810 (S, US). Guarapi, *Balansa* 3254 (L, P). In valley of Y-acá River, *Hassler* 6587 (GH, S). Near Igatimi, *Hassler* 5529a(S). Est. Caballero, *Anisits* 374 (S). Est. Santa Maria, *Anisits* 2412 (S). Central Paraguay, *Morong* 403 (US).

ARGENTINA: SALTA: ROSARIO DE LERMA: Campo Quijana, *Venturi* 8213 (GH). TUCUMÁN: Muñecas, *Schreiter* 1935 (S). FAMAILLA: San Pablo, *Venturi* 1175 (S, US). CAPITAL: Rio Sali, *Venturi* 1175a (GH, US). TAFI: Cumbre de Taficillo, *Venturi* 6047 (US). BURROYACO: Cerro del Campo, *Venturi* 10326 (S). FORMOSA: Laishi, *Jorgensen* 2324 (GH, US). MISIONES: Posadas, Bonpland, "La Granja," *Ekman* 181 (S), 182 (S, US). SAN IGNACIO: San Ignacio, *Vattuone & Bianchi* 143 (US); *Montes* 479 (UC). Gobernador Roca, *Montes* 562 (UC). CANDELARIA: Puerto Santa Ana, *Schwarz* 623 (UC). Loreto, *Montes* 439 (UC). Piaido Finlandesa, *Schwarz* 690 (UC). Arroyo "Martin chico," *Schwarz* s.n. (UC).

Because the differences between the varieties described in this species are so minor, and the transition between them so gradual, and because the varieties are more or less sympatric, I do not consider the varieties worthy of retention. However, in general, the species is hairier in the southern portion of its range than in the northern.

This species is most closely related to *M. hassleriana* Chod., but the pubescence, peduncles, and pedicels are generally longer in the latter species. *M. pilosa* usually has a longer terminal inflorescence, a greater total number of flowers, and more per cluster, and the flowers tend to be more frequent on the upper side of the branchlets; the flowers are rather evenly distributed in *M. hassleriana*.

M. pilosa is also related to *M. chamaedrys* St.-Hil. The major differences between them are mentioned under the description of the latter species.

13. Melochia hassleriana Chod. Bull. Herb. Boiss. II, 1:403. 1901.

Melochia ulmarioides St.-Hil. f. *sericea*, f. *Hassleriana* (Chod.), and f. *brevipedunculata*, all Schum. & Hassl. Bull. Herb. Boiss. II, 4:71. 1903.

Melochia ulmarioides St.-Hil. f. *albo-villosa* R. E. Fries, Svensk. Vet. Acad. Handl. 42(12):10. 1908.

An ascendent or procumbent suffrutex 0.5–1.5 meters high, with several stems from the base, the root woody, thickened, 0.7–1.0 cm. wide, the young stems and petioles pilose, hairs simple, straight, 1.5–4.0 mm. long, also shorter, recurved, 0.3–0.5 mm. long, internodes 1.5–7.0 cm. long; stipules 6–10.3 mm. long, 0.8–1.0 mm. wide, lance-

olate, ciliate and pilose or sericeous, hairs simple, 2–3.5 mm. long; petiole short, 0.1–1.0 cm. long.

Lamina 2.5–5.5 cm. long, 0.9–3.0 cm. wide, lanceolate to ovate, the base rounded, the apex acute, the upper surface sericeous-pilose, hairs tan, simple, 1.3–4.0 mm. long, the lower surface sericeous-pilose on the veins, hairs tan, simple, 1.7–4.0 mm. long, usually also stellate, 0.2 mm. long, between the veins, the margin long-ciliate, irregularly crenate-serrate, serrations 1.2–5.2 mm. wide, 0.6–1.5 mm. high, 8–13 pairs of straight, parallel primary veins, 2 are basal.

Inflorescences axillary, 3.5–5.5 cm. long, in the axils of the upper 2–4 leaves, also terminal, extending 3–6.5 cm. beyond the first leaf, the peduncle 0.5–3.0 cm. long, the ultimate divisions umbellate, 2–5 flowers per umbel, more than one umbel per peduncle, the pedicels 2.5–4.0 mm. long at anthesis, up to 6.0 mm. long in the fruiting state; bracts 3.5–9.5 mm. long, 0.3–1.5 mm. wide, lanceolate to nearly linear, ciliate and sericeous, hairs simple, 1–3 mm. long.

Calyx 6.3–7.8 mm. long, 3.4–4.4 mm. wide, not accrescent, pilose-sericeous and ciliate, hairs simple, 1–4 mm. long, also stellate, 0.1 mm. long, the teeth 3.7–5.5 mm. long, 1.4–1.8 mm. wide, deltoid-acuminate, the sinus acute; petals yellow to orange, 10–11.5 mm. long, 3.2–3.4 mm. wide, obovate-cuneate, attached to stamens for 1–1.5 mm., the claw 1 mm. long.

Longistylous form. Stamens 5.0 mm. long, the filaments united up to the anthers, the anther 1.2–1.3 mm. long, 0.6 mm. wide, oblong, emarginate at both ends, nearly to the middle from the apex; pistil 8.8 mm. long, the styles filiform, papillose for 1.2 mm. at the apex, free for 4.6 mm., united for 1.5 mm., the ovary ovoid, pentagonal, sericeous, hairs simple, 1–2 mm. long.

Brevistylous form. Stamens 7.4–7.8 mm. long, the filaments free for 4–5 mm., the anther 1.1–1.6 mm. long, 0.7 mm. wide, shape same as that above; pistil 5.5–6.0 mm. long, the styles papillose for 0.7 mm. at the apex, 2.2–2.5 mm. long, free to the ovary, the ovary ellipsoid to globular, pentagonal, sericeous, hairs simple, 1–2.3 mm. long.

Fruit 5 mm. long, 4.8 mm. wide, remnant of styles 1 mm. long, globular, obtusely pentagonal, the sulci between the carpels rather shallow, extending a fifth to a fourth the way to the center of the fruit, sericeous, hairs simple, 1–2 mm. long, also stellate, 0.1 mm. long, the stipe 0.5 mm. long; dehiscence all along the ventral suture and half way along the dorsal suture, also slightly septicidal; seeds 2.1–2.5 mm. long, 1.3–1.6 mm. wide, dark brown, 1 or 2 per cell.

Flowering specimens collected in October and December to March; fruiting ones, from December to March.

TYPE LOCALITY: The type was collected by *Hassler*, no. 1739, in thickets near Itacurubi, Paraguay. An isotype is cited below.

DISTRIBUTION: Paraguay and Paraná, Brazil, in campo, in sandy fields, in arid rocky places, at about 790 meters elevation.

BRAZIL: PARANÁ: Capão Bonito, *Dusén* 16903 (S).
PARAGUAY: Near Itacurubi, *Hassler* 1739 (NY, isotype). Along the road between Caacupé and Tobaty, *Archer & Rojas* 4856 (US). Road to Paraguay River, Hincinde ad Monte Calvario prope Villa occidental, *Lorentz* 33 (US). Capibary, *Hassler* 5917 (S). River Apa, *Hassler* 8074 (S, type of *Melochia ulmarioides* St.-Hil. f. *sericea* Schum. & Hassl.). Sierra de Maracaju, *Hassler* 5596 (S). In altaplanitie "Sierra de Amambay," *Hassler* 12038 (S). Near Igatimi, *Hassler* 4793 (S, type of *Melochia ulmarioides* St.-Hil. f. *brevipedunculata* Schum. & Hassl.), (W). Est. Armonia, *Anisits* 1913 (S, type of *Melochia ulmarioides* St.-Hil. f. *albo-villosa* R. E. Fries). San Luis between Rio Apa and Rio Aquidaban, *Fiebrig* 4451 (L).

This species has been misinterpreted as *Melochia ulmarioides* St.-Hil. I have seen the isotype of the latter species and consider it to be the same as *Melochia pilosa* (Mill.) Fawc. & Rendle.

This species is close to *Melochia pilosa* (Mill.) Fawc. & Rendle but differs in that the margins of the leaves are long-ciliate, the stems are usually less hairy, and the flowers are fewer and more loosely clustered. *M. pilosa* usually has a larger terminal inflorescence than *M. hassleriana*, and the flowers tend to be more frequent on the upper side of the branchlets but more evenly distributed in *M. hassleriana*.

14. Melochia chamaedrys St.-Hil. Fl. Bras. Mer. 1:161. 1825.

A small, procumbent or ascending, spreading herb to suffrutex 0.1–0.5 meter high, sometimes simple but usually with several slender shoots (2–10) from the root, the taproot thickened, woody, sometimes branched, 0.5–2.2 cm. wide, the young stems hirsute or rather densely covered with straight simple hairs 0.1–2.0 mm. long, curved simple ones 0.2–0.3 mm. long in a longitudinal line, and glandular ones 0.2–0.6 mm. long, internodes 1–3.3 (–7.5) cm. long; stipules 2.5–5.0 (–8.8) mm. long, 0.5–1.0 (–5.0) mm. wide, lanceolate, deltoid-acuminate or ovate, mostly ciliate, hairs simple, 0.2–2.0 mm. long, occasionally a few glandular, 0.2–0.3 mm. long; petiole 0.2–1.5 (–2.7) cm. long, indument similar to that of the young stems.

Lamina 1–4.3 (–6.5) cm. long, 0.8–3.0 (–4.5) cm. wide, ovate to nearly orbicular, rarely also oblong and lanceolate, the base rounded to cordate, the apex usually obtuse, sometimes also acute, the upper surface green, pilose, hairs scattered to rather dense, somewhat appressed, simple, usually also a few glandular, 0.1–1.6 mm. long, the lower surface green, similarly pubescent but more densely so, rarely stellate hairy, hairs 0.1–1.8 mm. long, the margin slightly irregularly crenate to crenate-serrate, crenations or serrations 0.5–3.2 mm. wide, 0.4–2.0 mm. high, 5–11 pairs of primary veins, 2 are basal.

Inflorescences axillary, (1.2–) 1.6–4.5 cm. long, in the axils of the upper 1–6 (–8) leaves and occasionally also terminal, extending 3.5 cm. beyond the first leaf, the ultimate divisions umbellate, few-flowered, 2–4 (–5) per umbel, the peduncle slender, 0.1–2.5 cm. long, sometimes absent, sometimes with a branch 0.4–0.5 cm. long, the pedicels slender, 1.6–9.3 mm. long, mostly glandular, hairs 0.1–0.4 mm. long; bracts, 0.6–4.0 (–8.3) mm. long, 0.1–1.3 (–4.8) mm. wide, lanceolate to ovate or linear, mostly ciliate, hairs simple, 0.1–1.7 mm. long.

Calyx 4.6–7.8 (–8.5) mm. long, 3.1–4.8 (–5.1) mm. wide, not accrescent, sericeous and ciliate, hairs simple and usually also glandular, 0.1–0.8 (–1.6) mm. long, the teeth 2.5–5.0 mm. long, 1.2–1.8 (–2.5) mm. wide, deltoid- to ovate-acute or ovate-acuminate, the sinus acute; petals yellow to orange, Weberbauer no. 6220 from Peru was rose with brown veins according to Macbride (39), 7.2–11 mm. long, 2.7–4.1 mm. wide, obovate-cuneate, attached to the staminal tube for 0.5–1.0 mm., the claw 0.9–1.8 mm. long, 5 minute glands sometimes present between the bases of the petals.

Longistylous form. Stamens 3.8–4.2 mm. long, the filaments united up to the anthers or separate for 0.5 mm., the anther 0.9–1.2 mm. long, 0.5–0.8 mm. wide, oblong, emarginate at both ends, nearly to the middle from the apex; pistil 4.8–7.5 mm. long, the styles filiform, free for 2.0–5.3 mm., united for 0.3–1.0 mm., papillose at the apex for 1 mm., the ovary ovoid to globular, pentagonal, hirsute to sericeous at the apex, hairs simple, 0.1–1.2 mm. long.

Brevistylous form. Stamens 6.1–8.2 mm. long, the filaments free for 3.2–5.1 mm., the anther 1.1–1.6 mm. long, 0.6–1.1 mm. wide, shape the same as that above; pistil 4–5 mm. long, the styles 2 mm. long, free to the ovary or united for 0.7 mm., papillose for 0.3–0.5 mm. at the apex, the ovary ovoid, pentagonal, hirsute-sericeous, mostly near the apex, hairs 0.2–1.3 mm. long.

Fruit 4.4–5.6 mm. long, 4.4–4.8 (–5.3) mm. wide, globular, sometimes suboblong, obtusely pentagonal, the sulci between the carpels shallow to moderately deep, extending a fifth to a third the way to the center of the fruit, covered with simple hairs 0.1–1.5 mm. long, sometimes a few forked and glandular hairs 0.1–0.4 mm. long, the base narrowed to a stipe 0.5–1.0 mm. long; dehiscence all along the ventral suture, a third to half way along the dorsal suture, and slightly septicidal; seeds 1.5–2.6 mm. long, 1.1–1.5 mm. wide, trigonal, dark brown, rugulose, 2 per cell.

Flowering specimens collected in August, September, November to February, April, and May; fruiting ones, in September, November to February, and April.

Key to Varieties of *M. chamaedrys*

1. Lamina suborbicular, 1–2.3 cm. long, 0.9–2.7 cm. wide, apex obtuse, crenations up to 2 mm. high; pedicels 2.5–9.3 mm. long.
14a. M. chamaedrys var. **chamaedrys**

1. Lamina ovate, 1.2–4.5 (–6.5) cm. long, 0.8–3.0 (–4.5) cm. wide, apex usually acute, crenations up to 1.2 mm. high; pedicels 1.6–3.0 mm. long.
14b. M. chamaedrys var. **decumbens**

14a. Melochia chamaedrys St.-Hil. var. **chamaedrys**
Riedleia Chamaedrys (St.-Hil.) G. Don, Gen. Syst. 1: 529. 1831.
Melochia chamaedrys St.-Hil. f. *typica* Ekman, Arkiv. Bot. 9(4): 46. 1910.
Melochia chamaedrys St.-Hil. var. *loretensis* and var. *viscidula*, both Hassl. Addenda Pl. Hassl. 12. 1917 (without description).

Commonly, this variety is 0.1–0.3 meter long; stipules, 2.5–3.6 mm. long, 0.5–0.8 mm. wide; petiole 0.2–0.9 cm. long; lamina 1–2.3 cm. long, 0.9–2.7 cm. wide, nearly orbicular, the apex obtuse, the crenations, up to 2.0 mm. high, 5–7 pairs of primary veins; inflorescences 1.6–3.5 cm. long, the peduncle 0.6–1.7 cm. long, the pedicels 2.5–9.3 mm. long, the bracts 0.6–2.5 mm. long, 0.1–0.5 mm. wide.

TYPE LOCALITY: The type was collected by St.-Hilaire in herbaceous fields near the estate commonly called Estancia do Salto S. Itaroro, not far from the village of S. Francisci Borjensis, Misiones, Argentina. The isotype is cited below.

DISTRIBUTION: Peru, Brazil, Uruguay, Paraguay, and Argentina, in shrubby and herbaceous fields, in dry compo, on hills among dry calcareous rocks, and in thickets among rocks, at 60–800 meters elevation.

PERU: CAJAMARCA: JAEN: Near the confluence of Chinchipe and Marañon *Weberbauer* 6220 (US).

BRAZIL: BAHIA: Catinga de Moura, *Schreiner* in 1890 (R 78127). MATO GROSSO: Capão Bonito, *Archer & Gehrt* 86 (US). PARANÁ: PARANA: Campo Mourão: Rio da Vargem, *Hatschbach* 8757 (US). SANTA CATARINA: Campos Novos: 34 km. E. of Joaçaba, *L. B. Smith & Klein* 11181 (US). RIO GRANDE DO SUL: Campinas near Sta. Rosa, *Spies* (PACA 36029). Caaró near S. Luiz, *Rambo* 3056 (PACA), (PACA 53298), (PACA 53433). Cerro Largo near S. Luiz, *Buck* (PACA 11136). Livramento, *Rambo* 3950 (PACA). Parecí near Montenegro, *Rambo* (PACA 42973).

URUGUAY: SALTO: Arapey, *Herter* 2293 (S).

PARAGUAY: Villa Encarnacion, *Rojas* 7924 (S). Itapé, in canyon at the foot of Cordillera de Villarrica, *Jorgensen* 4477 in part (S), 4477 (A, US).

ARGENTINA: CORRIENTES: SANTO TOMÉ: Est. "Garruchos," *Pedersen* 971 (S, US). MISIONES: Near Est. do Salto S. Itaroro near S. Francisci Borjensis, *St.-Hilaire* (P, isotype). ?MISIONES: F neg. 9600 ex B, presumably an isotype of the species. Posadas, *Ekman* 183 (S), 184 (S). CANDELARIA: Loreto, *Montes* 560 (S).

This species is close to *Melochia pilosa* (Mill.) Fawc. & Rendle, but the latter is more robust. *M. pilosa* is erect and 0.4–3.0 meters high;

M. chamaedrys is procumbent or ascending and 0.1–0.5 meter high. The leaves are often suborbicular, those of *M. pilosa* are more elongate, usually ovate to lanceolate, and larger. The inflorescences are primarily axillary but primarily terminal in *M. pilosa*.

14b. Melochia chamaedrys St.-Hil. var. **decumbens** (Fries) A. Goldberg, comb. et. stat. nov.

Melochia decumbens R. E. Fries, Svensk. Vet. Akad. Handl. 42(12):11. 1908.
Melochia chamaedrys St.-Hil. f. *decumbens* Ekman, Arkiv. Bot. 9(4):46. 1910.

This variety is more robust than the typical variety. It is up to 0.5 meter long; stipules 4–5 (–8.8) mm. long, 0.7–1.0 (–5.0) mm. wide; petiole 0.2–1.5 (–2.7) cm. long; lamina more densely hairy than that of the typical variety, 1.2–4.5 (–6.5) cm. long, 0.8–3.0 (–4.5) cm. wide, ovate, the apex usually acute, crenations to 1.2 mm. high, 5–11 pairs of primary veins; inflorescences 1.2–4.5 cm. long, the peduncle (0–) 1–2.5 cm. long, the pedicel 1.6–3.0 mm. long, the bracts 2.6–4.0 (–8.3) mm. long, 0.6–1.3 (–4.8) mm. wide.

TYPE LOCALITY: The syntypes were collected by Anisits, nos. 2509 and 2656, at Estancia Santa Maria, Paraguay. The latter is selected as lectotype.

DISTRIBUTION: Paraguay and Argentina on dry, calcareous, rocky hills.

PARGUAY: Estancia Santa Maria, *Anisits* 2509 (S, paratype), 2656 (S, lectotype, also US neg. 5617, syntypes of *Melochia decumbens* Fries).

ARGENTINA: MISIONES: Posadas, Bonpland, *Lilliesköld* s.n. (S, also US neg. 5618).

Ekman (see synonymy) considered *Melochia decumbens* Fries to be a form of *Melochia chamaedrys* St.-Hil. I consider it sufficiently distinct to have varietal status.

15. Melochia kerriifolia Triana & Planch. Ann. Sci. Nat. IV, 17:341. 1862.
Melochia Humboldtiana Steyerm. Fieldiana, Bot. 28(2):365. 1952.

An erect, slender-branched annual herb or suffrutex 0.2–0.8 meter high, the root not thickened, the young stems hirsute, hairs scattered and sometimes in a longitudinal line, simple, straight, and shorter recurved hairs and very few glandular hairs, 0.2–1.3 mm. long, internodes 1–11 cm. long; stipules 1.5–4.0 mm. long, 0.3–1.2 mm wide, deltoid-acute to deltoid-acuminate or lanceolate, mostly ciliate, hairs simple, 0.2–1.3 mm. long; petiole 0.1–2.3 cm. long, tomentose, especially on the adaxial surface, hairs mostly simple, some forked, few glandular, 0.5–1.8 mm. long.

Lamina 0.8–9.3 cm. long, 0.2–3.1 cm. wide, narrowly lanceolate to ovate, the base rounded to subcordate, the apex acute to slightly acuminate, the upper surface subglabrous, with a few simple, appressed or recurved hairs 0.1–1.0 mm. long on the midrib, and some-

times a few glandular hairs, especially on the margin, the lower surface with scattered, appressed, simple hairs 0.1–1.1 mm. long on the veins, the margins irregularly crenate-serrate to serrate, serrations 0.8–4.2 mm. wide, 0.5–1.9 mm. high, 5–14 pairs of primary veins, 1 or 2 are basal.

Inflorescences 1–21 cm. long, terminal and axillary, rarely also leaf-opposed, in the upper 1–4 axils, or on axillary branches up to 7.3 cm. long, with reduced leaves, slender, usually paniculate, the ultimate divisions umbellate, 2 or 3 (1–5) flowers per umbel, the peduncle slender, 0.6–8.5 cm. long, the pedicels 1.5–5.0 mm. long, with scattered glandular hairs; bracts 1–3.5 mm. long, 0.2–0.8 mm. wide, deciduous, deltoid-acute to deltoid-acuminate or lanceolate, mostly ciliate, hairs simple, 0.2–0.8 mm. long.

Calyx 3.0–4.7 mm. long, 2.4–4.0 mm. wide, not accrescent, hirsute and sometimes also ciliate, hairs simple, some glandular, rarely a few forked, 0.1–1.2 mm. long, the teeth 2.2–3.3 mm. long, 0.8–1.4 mm. wide, deltoid-acuminate, the sinus acute to narrowly rounded; petals yellow, 5.0–8.3 mm. long, 2.2–3.1 mm. wide, obovate, obovate-cuneate, or nearly elliptic, the claw 0.5–1.0 mm. long, attached to the stamens for 0.3–1.0 mm.

Longistylous form. Stamens 2.5–3.2 mm. long, the filaments united up to the anthers, the anther 0.8–1.1 mm. long, 0.4–0.6 mm. wide, oblong, emarginate at both ends, nearly to the middle from the apex, sacs slightly divergent at the apex, rarely 6 stamens; pistil 2.8–3.5 mm. long, the styles 1.2–1.7 mm. long, free to the ovary, filiform, papillose for 0.5–0.7 mm. at the apex, the ovary ovoid to globular-pentagonal, hirsute-sericeous, hairs simple and sometimes also forked and a few stellate, 0.2–0.7 mm. long, rarely 6 carpels, stipe none but base of carpels narrowed for 0–0.5 mm.

Brevistylous form not seen.

Fruit usually in pairs, 3.7–5.5 mm. long, 3.5–5.6 mm. wide, globular to somewhat oblong, obtusely pentagonal, the sulci between the carpels shallow, extending a fifth to a fourth the way to the center of the fruit, hiruste to tomentulose, hairs simple and sometimes forked and stellate, 0.1–1.0 mm. long, base narrowed to a stipe 0.5–1.0 mm. long; dehiscence all along the ventral suture and a third to half way along the dorsal suture, slightly septicidal to completely septicidal and the fruit falling apart; seeds 1.9–2.8 mm. long, 1.2–2.0 mm. wide, brown to black, trigonal, 2 per cell.

Flowering specimens collected in May, June, October, and November; fruiting ones, from April to June, and in October and November.

TYPE LOCALITY: Savannas d'Ibagué, basin of the Magdalena, Colombia, elevation 1,300 meters. Type collected by Triana, cited below.

DISTRIBUTION: Mexico, Guatemala according to Standley & Steyermark (56), Venezuela, Colombia, and Brazil, in llanos and fields, on rocky open limestone slopes at 20–1,300 meters elevation.

MEXICO: VERACRUZ: Zacuapan, *Purpus* 8031 (UC). Zacuapan, Fortin, *Purpus* 2048 (GH, US). Camarón, *Purpus* 11066 (US). OAXACA: TUXTEPEC: Chiltepec and vicinity, *Martinez-Calderón* 506 (A, US).

VENEZUELA: SUCRE: Between Cocollar and Guamal, *Steyermark* 62436 (F, isotype of *Melochia Humboldtiana* Steyerm., also US neg. 5671).

COLOMBIA: MAGDALENA: Santa Marta, *H. H. Smith* 484 (A, S, US). TOLIMA Ibagué, Mariquita, *Triana* (P, type, also US neg. 5659; F fragment and neg. 23860 of type; W).

BRAZIL: Near border between Pará and Goiás, *Burchell* 9055 (GH). MATO GROSSO: Corumbá, *Malme* 3042 (S).

This species is usually characterized by a loose terminal inflorescence. The fruits usually develop in pairs and the leaves are subglabrous. It is close to *M. pilosa* (Mill.) Fawc. & Rendle, but the inflorescence is much more lax, the leaves are not as hairy, and the calyx is shorter. The fruits of *M. pilosa* are not in pairs.

Steyermark distinguishes his *M. Humboldtiana* from *M. kerriifolia* by slight differences in vestiture.

16. Melochia argentina R. E. Fries, Meded. Rijk. Herb. Leid. No. 19: 42. 1913.

Melochia argentina Hassl. Repert. Sp. Nov. Fedde 13:237. 1914.

Melochia argentina Hassl. var. *genuina* Hassl. Repert. Sp. Nov. Fedde 13:238. 1914.

Melochia argentina Hassl. var. *lanceolata* Hassl. Repert. Sp. Nov. Fedde 13:238. 1914.

A branched subshrub to shrub 0.6–2.5 meters high, the young stems hirsute in longitudinal lines, hairs simple, curved, 0.1–0.3 mm. long, internodes 1–3.5 cm. long; stipules 3.6–7.5 mm. long, 0.2–1.0 mm. wide, deltoid-acuminate to nearly linear, with few simple hairs, mostly ciliate, 0.1–0.3 mm. long; petiole 0.8–2.5 cm. long, vestiture similar to that of the young stems, but sometimes encircling the petiole.

Lamina 2.5–7.8 cm. long, 1.5–3.6 cm. wide, up to 9 by 4 cm. according to Hassler (24), usually ovate, also ovate-lanceolate to lanceolate, the base rounded, the apex acute to subacuminate, the upper surface subglabrous, hairs simple appressed, 0.1–0.6 mm. long on the midrib and sometimes present between the veins, the lower surface glabrous or with few simple appressed hairs 0.1–0.5 mm. long on the veins, the margin irregularly crenate-serrate, serrations relatively high, 2–8.5 mm. wide, 0.7–3.6 mm. high, 6–9 pairs of primary veins, 2 are basal.

Inflorescences axillary, 1–4.8 cm. long, at 1–14 upper nodes, rarely also terminating axillary branches 4–13.5 cm. long, the terminal inflorescence of a branch extending 3–4 cm. beyond the first leaf, the

ultimate divisions umbellate with 2 or 3 (3–6, Hassler) flowers per umbel, 1–4 umbels per inflorescence, the peduncle 0–3.3 cm. long, with a branch 0–0.5 cm. long, the pedicels 1–4 mm. long; bracts 1.3–3.7 mm. long, 0.2–0.5 mm. wide, deltoid-acuminate to acicular, mostly ciliate, hairs simple, 0.1–0.3 mm. long.

Calyx 5.5–7.5 mm. long, 4.7–5.8 mm. wide, not accrescent, mostly ciliate, hairs simple, 0.1–0.2 mm. long, the teeth 2.5–3.6 mm. long, 1.8–2.8 mm. wide, deltoid-acuminate or deltoid-acute, the sinus acute; petals yellow, 8.6–9.6 mm. long, 3.5–5.0 mm. wide, 10–12 by 5–7 mm. according to Fries, obovate-cuneate, the claw 0.5 mm. long, attached to the stamens for 0.5 mm.

Longistylous form not seen.

Brevistylous form. Difference in length of gynoecium and androecium not marked, stamens 4.8–5.6 mm. long, the filaments free for 0.5–1.5 mm., the anther 1.7–2.1 mm. long, 1.0 mm. wide, oblong, emarginate at both ends, almost to middle from the apex, pollen larger than average for the genus; pistil 4.2–5.1 mm. long, the styles free for 1.5–2.2 mm., united at the base, papillose at the apex for 0.7 mm., the ovary ovoid, hirsute, hairs simple and forked, 0.1–0.7 mm. long, stipe none.

Fruit 6.5–7.5 mm. long, 4.5–6.5 mm. wide, obtusely pentagonal, globose, acute to subacuminate at the apex, moderately deeply sulcate between the carpels, but the sulci extending less than half way to the center of the fruit, sparsely hirsute, hairs simple and forked, 0.2–0.5 mm. long, stipe none; dehiscence all along the ventral suture and one-third along the dorsal suture, also slightly septicidal, but capsule not falling apart, several loose fibers about 1 mm. long along the ventral sutures; seeds 2.6–2.8 mm. long, 1.5–1.6 mm. wide, brown, sometimes with short white longitudinal markings.

Flowering specimens collected in October, November, and January to March; fruiting ones, in October, November, January, and February.

TYPE LOCALITY: Salta, Argentina, in moist places in the forest between Embarcacion and Miraflores. Type collected by Herzog, no. 1029, cited below.

DISTRIBUTION: Tarija, Bolivia to Cordoba, Argentina, in moist places in forests, thickets on hillsides, and in dry gravel of riverwash, at 650–1,700 meters elevation.

BOLIVIA: TARIJA: La Merced at Bermejo, *Fiebrig* 2190 (S).

PARAGUAY: Ibytymi, *Rojas* 13282 (S).

ARGENTINA: JUJUY: Cerro de Zapla, *Venturi* 5122 (US). LEDESMA: Sierra de Calilegua, *Venturi* 5348 (US). SAN PEDRO: About 17 km. SW. of San Pedro de Jujuy, *Eyerdam & Beetle* 22573 (GH). SALTA: Between Embarcacion and Miraflores, *Herzog* 1029 (L; S, type; F neg. 9598 ex B in US). Capital, *Schulz*

900 (S). ORÁN: Caraparí, *Bridarolli* 3267 (GH). Obra Grande, *Venturi* 5576 (S, US). TUCUMÁN: TAFI: Yerba Buena, *Venturi* 160 (US); *Wall* 12 (S).

This species is characterized by its rather large fruits, among the largest in the section *Mougeotia*, and very reminiscent of those in the section *Visenia*, by subglabrous leaves with high serrations, and by the nearly equal length of the gynoecium and the androecium.

From their descriptions and the fact that each cited *Stuckert* 12757 as belonging to his species, it is evident that Fries' and Hassler's species are the same. Hassler (24) separated *Melochia argentina* var. *lanceolata* Hassler from the type on the basis of the shape of the leaf. Since ovate and lanceolate leaves may occur on the same plant, I do not consider that, in this species, a variety based on the shape of the leaf is worthy of recognition.

17. Melochia ulmifolia Benth. *in* Hook. Journ. Bot. 4:129. 1841.
Riedleia ramuliflora Miq. Linnaea 19:132. 1847.
Riedleja dichotoma Turcz. Bull. Soc. Nat. Mosc. 31(1):208. 1858.
Melochia Benthami Schum. *in* Mart. Fl. Bras. 12(3):40, pl 7. 1886.
Melochia carthaginensis Willd. ex Schum. *in* Mart. Fl. Bras. 12(3):40. 1886.
Melochia ramuliflora (Miq.) R. E. Fries, Kgl. Svensk. Vet. Akad. Handl. 42(12):11. 1908.

A scrambling shrub to small tree 1.8–4.0 meters high, the young stems and petioles tomentulose, hairs stellate, 0.1–0.2 mm. long, the internodes 1.8–5.5 cm. long; stipules caducous, 1.7–2.5 mm. long, 0.2–0.6 mm. wide, deltoid-acuminate to nearly linear, hirsute on the abaxial surface, hairs 0.1–0.4 mm. long; petiole 1–3.1 cm. long, slightly broadened at the distal end.

Lamina relatively large, 5.0–14.0 cm. long, 2.0–8.2 cm. wide, ovate to oblong-ovate, the base rounded, truncate or subcordate, the apex acute to slightly acuminate, the upper surface green, with scattered, nonoverlapping, stellate hairs 0.1–0.2 mm. long on the veins and usually between them, the lower surface green, puberulous, velvety to the touch, hairs stellate, 0.2–0.3 mm. long, the margin irregularly crenate-serrate, serrations 2–4.5 mm. wide, 1–2.5 mm. high, 6–9 pairs of primary veins, 2 are basal, one more prominent than the other, prominent beneath.

Inflorescences axillary, at up to 8 upper nodes, up to 6 cm. long and 5 cm. broad, open, 3–8 flowers per umbel, 3–8 umbels at each axil, the peduncle 0.2–1.0 cm. long, sometimes with a primary branch 0.6 cm. long, and a secondary one 0.3–0.7 cm. long, the pedicel 1–5 mm. long; bracts 1–3 mm. long, 0.2–0.5 mm. wide, deltoid-acuminate to nearly linear, hirsute-tomentulose, hairs 0.1–0.3 mm. long; flowers very fragrant.

Calyx 4.3–6.1 mm. long, 3.7–5.7 mm. wide, campanulate, not accrescent, tomentulose, hairs forked and stellate, 0.1–0.6 mm. long,

the teeth 1.5–2.9 mm. long, 1.3–2.5 mm. wide, deltoid-acute, deltoid-acuminate to ovate, the sinus acute to somewhat rounded; petals white, yellowish white or yellow, 4.4–5.5 mm. long, 1.7–2.3 mm. wide, obovate to obovate-oblong, or oblanceolate, separate from one another and from the androecium, the blade rather sharply demarcated from the claw, claw 0.5–1.0 mm. long, hairs at the base of the adaxial surface of the blade 0.1–0.2 mm. long.

Longistylous form. Stamens 3.2–4.0 mm. long, the membrane between the filaments very thin, hairs near the base 0.6–0.8 mm. long or absent, the filaments free for 0.5–1.0 mm., the anther 0.8–1.2 mm. long, 0.7–0.8 mm. wide, oblong, emarginate at both ends; pistil 4.5–5.2 mm. long, the styles 2.7–3.7 mm. long, free to the ovary, hirsute at the base, papillose at the apex for 0.7 mm., the ovary oval to ovoid, hirsute mostly on its angles, hairs 0.5–1.0 mm. long, stipe none.

Brevistylous form. Stamens 5.5 mm. long, the filaments free for 3.5 mm., hairs at the base of the filaments 0.1–0.2 mm. long, the anther 1.1 mm. long, 0.6 mm. wide; pistil 3.0–3.5 mm. long, the styles free to the ovary, 1.7 mm. long, the ovary ovoid, hirsute, hairs up to 1.2 mm. long.

Fruit a capsule 5–6 mm. long, 4.8–5.5 mm. wide, nearly globular, mucronate at the apex, obtusely pentagonal, very shallowly sulcate between the carpels, hirsute-tomentulose, hairs 0.1–1.0 mm. long, the stipe 0.2–0.3 mm. long; dehiscence all along the ventral suture and 0.2–0.25 the way along the dorsal suture, only slightly septicidal; seeds 1.9–2.4 mm. long, 1.1–1.2 mm. wide, trigonal, brown.

Flowering specimens collected in February, May, June, and from August to December; fruiting ones, in February, May, June, August, and from October to December.

TYPE LOCALITY: British Guiana, in savannas. Isotypes collected by Schomburgk, no. 203, cited below.

DISTRIBUTION: Santander, Colombia to Maranhão, Brazil, in second-growth thickets, along trails, on river banks, at the edge of clearings, in fields, on loamy soil, at 80–700 meters elevation.

FRENCH GUIANA: ?*Le Prieur* 302 (P). *Melinon* 166 (P), 277 (P), 487 (P). Banks of River Maroni, *Melinon* 210 (P), 229 (P, US); *Sagot* 1072 (P).

SURINAM: *Hostmann* 226 (US). *Hostmann & Kappler* 1047 (S, W, isotypes of *Riedleja dichotoma* Turcz.). Near Victoria station in region on way to Surinam River, *Kappler* 1695 (P, S). Near Blaauwe Berg, *Splitgerber* 890 (L).

BRITISH GUIANA: *Schomburgk* 203 (L, isotype). Orealla, Courantyne River, *Forest Dept.* 6753 (MICH, S).

VENEZUELA: BOLÍVAR: La Unión, Medio Caura, *Ll. Williams* 11235 (US).

COLOMBIA: SANTANDER: Vicinity of Puerto Araujo on Carare River, *Haught* 1705 (US). Between Nariño and El Tambor, *Killip & Smith* 14948 (US).

BRAZIL: RIO BRANCO: Furo do Cujubim, *Kuhlmann* 126 (US). AMAZONAS: Madeira, ?Itapisuiua, *Kuhlmann* 243 (RB). PARÁ: Baião, Tocantins, *Kuhl-*

mann 2093 (US). Rio Cupary, affl. do Tapajoz, *Kuhlmann* 1953 (US). Rio Erepecurú, *Sampaio* 4991 (R, US), 5567 (R, US). Marabá, *Pires* 4522 (US). Between S. João de Araguaya, S. Anna, *Burchell* 9264 (P). MARANHÃO: Turyassú, *Snethlage* 272 (US). Fazenda do Rosario, *Lisboa* 55 (US).

Perhaps this species approaches most closely the section *Visenia* of Asia and the Pacific Islands in habit, leaves, inflorescence, and fruit. It is characterized by having hairs at the base of the petal blade, by open, branched, fairly large axillary inflorescences, by large leaves sparsely hairy on the upper surface, and by dehiscence of the fruit part way along the dorsal suture and the entire ventral suture. It is one of the largest species of the section *Mougeotia*.

Schumann (47) in monographing *Melochia* of Brazil considered *Melochia ulmifolia* St.-Hil. & Naud. and *Melochia ulmifolia* Benth., based on different types, to have been published in 1842. He retained the name for the former on the basis of page priority and renamed Bentham's species *Melochia Benthami*. However, as explained by Sprague (50), Bentham published his species in 1841 and therefore the name should be applied to his species. R. E. Fries (15) pointed out that Bentham's species had been described under the names *Riedleia ramuliflora* Miq. in 1847 and *Riedleja dichotoma* Turcz. in 1858. He proposed for it the new combination *Melochia ramuliflora* (Miq.) R. E. Fries. Since he admits that Bentham was the first to describe the species, his action is unacceptable.

18. Melochia gardneri Sprague, Kew Bull. 124. 1915. PLATE 1
Melochia ulmifolia St.-Hil. & Naud. Ann. Sci. Nat. II, 18:36. 1842; non Benth. 1841.

A branched, erect, slender shrub 1.8–2.4 meters high, the young stems and petioles tomentulose, hairs stellate, average 0.2 mm. (0.1–0.7 mm.) long, internodes 1.3–3.4 cm. long; stipules 3.2–4.0 mm. long, 0.6–1.2 mm. wide, deltoid-acuminate, tomentulose and ciliate, hairs stellate and simple, 0.2–0.6 mm. long; petiole 0.7–2.4 (–3.5) cm. long.

Lamina rather thin, 5.7–8.8 (–12) cm. long, 2.8–5.0 (–6.8) cm. wide, ovate to ovate-lanceolate, the base rounded, the apex acute to acuminate, the upper surface green, sericeous, majority of hairs simple, fewer shorter, forked and stellate, 0.2–1.3 mm. long, the lower surface lighter green, tomentulose, soft to the touch, hairs stellate, a few simple, 0.2–0.7 mm. long, the margin irregularly crenate-serrate, serrations rather high, 0.8–3.6 mm. wide, 0.5–2.6 mm. high, 10–12 pairs of primary veins, 2 are basal.

Inflorescences terminal, sometimes also axillary, spicate, dense, extending 4–5 cm. beyond the first leaf, the axillary ones 1 cm. long, the pedicels 1–2 mm. long; bracts 3.5–5.7 mm. long, 0.5–0.7 mm. wide lanceolate, sericeous on dorsal surface and ciliate, longer hairs simple, shorter ones stellate, 0.2–0.7 mm. long.

Calyx 7–8.3 mm. long, 4.3–4.4 mm. wide, not accrescent, hairs most abundant on the junctures of the sepals, and ciliate, stellate, 0.1 mm., forked and simple, 0.5–1.2 mm. long, the teeth 3.5–4.5 mm. long, 2–2.2 mm. wide, deltoid-acuminate, the sinus acute; petals ?purple (dried), 11.6–12 mm. long, 2.5–3.1 mm. wide, up to 4 mm. wide according to Schumann (47), oblanceolate, the claw rather long, 3–4 mm. long, attached to the stamens for 2.7 mm.

Longistylous form. Stamens 4.9–5.9 mm. long, the filaments united up to the anthers, the anther 1.3–1.4 mm. long, 0.6–0.7 mm. wide, oblong, emarginate at both ends; pistil 11.1–12 mm. long, the styles free for 4–4.7 mm., united for 3.5–4.0 mm., the ovary globose, pentagonal-ovoid, the ovary and half of the free portion of the styles stellate tomentulose.

Brevistylous form not seen.

Fruit 7 mm. long, gradually aristate for about 1 mm., 4.6 mm. wide, globular-ovoid, obtusely pentagonal, pointed at the apex, shallowly sulcate between the carpels, tomentulose, stellate hairs 0.1–0.2 mm., forked hairs 0.4–0.7 mm. long, stipe none; dehiscence all along the ventral suture and a third along the dorsal suture, slightly septicidal; seeds (not ripe) 2.5–2.8 mm. long, 1.5–1.8 mm. wide, brown, chalazal membrane 0.2–0.3 mm. long, almost winglike, 2 per cell.

Flowering and fruiting specimens collected in April.

TYPE LOCALITY: Brazil, Goiás, in woods on the Serra de Santa Brida. Type in Herbarium Delessert, collected by Gardner, no. 3608, isotype cited below.

DISTRIBUTION: Brazil, Goiás, in woods; also Piauí according to Schumann (47).

BRAZIL: GOIÁS: Serra de Santa Brida, *Gardner* 3608 (P, isotype, also US neg. 5665 ex P, and F neg. of type at G).

This species is characterized by its dense, unbranched terminal spike, rather large, thin, broad leaves, and comparatively large fruit for the section *Mougeotia*, dehiscent part way along the dorsal suture in addition to the entire ventral suture. It appears to be most closely related to *Melochia pilosa* (Mill.) Fawc. & Rendle.

As explained by Sprague (50), Bentham's *Melochia ulmifolia* was published prior to that of St.-Hilaire and Naudin. Sprague renamed the latter species *Melochia Gardneri* Sprague. In accordance with recommended practice, I have substituted the small "g" for the capital "G" in *Gardneri*.

19. Melochia mollis (H.B.K.) Triana & Planch. Ann. Sci. Nat. IV, 17:343. 1862.
Mougeotia mollis H.B.K. Nov. Gen. & Sp. 5:328. 1823.
Riedleia mollis (H.B.K.) DC. Prodr. 1:491. 1824.
Visenia mollis (H.B.K.) Spreng. Syst. 3:30. 1826.
Riedleia multiflora Presl, Rel. Haenk. 2:147. 1835.

Anamorpha melochioides Triana & Karst. *in* Triana, Nuev. Jen. i Esp. Fl. Neo-Granad. 10. 1854.
Melochia globifera Triana & Planch. Ann. Sci. Nat. IV, 17:342. 1862.

Usually a shrub, sometimes herb, erect, 0.5–5.0 meters high, the young stems and petioles densely tomentulose-villous, hairs brownish, stellate and usually also forked and simple, 0.1–2.0 mm. long, woolly to the touch, internodes 1.1–8.0 cm. long; stipules 3–8.5 (–10.0) mm. long, 0.7–1.8 (–3.8) mm. wide, deltoid-acuminate or deltoid-acute, lanceolate or ovate, tomentulose and sometimes ciliate, hairs stellate (short), forked and sometimes also simple, 0.2–1.5 mm. long; petiole 0.5–5.4 (–8.0) cm. long.

Lamina 3.7–13.5 (–22) cm. long, 2–8.8 (–10.5) cm. wide, broadly ovate to lanceolate-ovate, the base rounded to cordate, the apex acute to slightly rounded or slightly acuminate, the upper surface usually greenish, sometimes brownish due to the hairs, tomentulose, sericeous or with scattered hairs, velvety to the touch, hairs stellate (short) and sometimes also forked and simple, 0.2–1.5 mm. long, sometimes appressed, the lower surface tomentulose, velvety or woolly to the touch, hairs stellate, sometimes a few forked and simple, 0.2–1.2 mm. long, lighter green, or yellowish-tan canescent, the margin irregularly crenate-serrate, serrations 0.6–5.5 mm. wide, 0.4–3.0 mm. high, 7–11 (–15) pairs of primary veins, 2 (–3) are basal.

Inflorescences 2–10.5 cm. long, axillary in the upper 2–11 or more axils, rarely also terminal, in subcapitate umbels of 2–5 flowers, 4–6 umbels in an inflorescence, sometimes corymbiform or paniculate, the peduncle relatively thick, (0.2–) 0.5–8.0 cm. long, 0.5–1.5 mm. wide, sometimes with a primary branch 0.8–3.5 cm. long, and rarely a secondary one 1–1.5 cm. long, sometimes naked branches with peduncles at 4–5 nodes, the pedicels 1–4 (–8) mm. long; bracts 1–6.2 mm. long, 0.2–2.2 mm. wide, deltoid-acuminate to linear, tomentulose and sometimes ciliate, hairs stellate, forked, and simple, 0.1–1.4 mm. long.

Calyx 4–6.8 mm. long, 3.3–6.0 (–6.5) mm. wide, the teeth 1.7–4.6 mm. long, 1.2–2.7 mm. wide, deltoid to subovate, acute to acuminate, the sinus acute, sometimes accrescent, becoming 7–9.5 mm. long, 7.7–10.0 mm. wide, the teeth 4.5–5.5 mm. long, 3.5–5.5 mm. wide, densely tomentulose, canescent, hairs stellate (short) and sometimes also forked and simple, 0.2–1.0 mm. long; petals white to pale yellow or white distally and yellow proximally, 4.2–6.8 mm. long, 1.4–2.7 mm. wide, obovate, obovate-oblong, obovate-lanceolate, or oval, the claw 0.4–1.0 mm. long, free from the staminal tube or attached to it for 0.5 mm., sometimes 2 or 3 simple and forked hairs 0.1 mm. long just above the claw.

Longistylous form. Stamens 3.2–4.2 mm. long, the filaments united up to the anthers, sometimes tufts of hairs 0.4–0.5 mm. long

at the base of the staminal tube, alternate with the filaments, hairs 0.1 mm. long, the anther 1.0–1.3 mm. long, 0.5–1.0 mm. wide, oblong, emarginate at both ends, nearly to the middle from the apex, sacs slightly divergent at the apex; pistil 4.1–6.3 mm. long, the styles 2.6–4.0 mm. long, free to the ovary, filiform, slightly clavate and papillose at the apex for 0.7–1.0 mm., the styles and ovary densely tomentulose, hairs stellate and sometimes also simple, 0.2–0.3 mm. long, the ovary globose.

Brevistylous form. Stamens 4.3–5.4 mm. long, the filaments free for 1.5–2.5 mm., the anther 0.8–1.3 mm. long, 0.4–0.7 mm. wide, shape same as that above, staminode teeth 0.1–0.2 mm. long sometimes present; pistil 2.8–3.8 mm. long, the styles 1.2–2.2 mm. long, free to the ovary, papillose for 0.6 mm., base of the styles and the ovary densely tomentulose, hairs stellate, 0.1–0.3 mm. long.

Fruit 2.7–4.0 mm. long, 3.3–4.8 mm. wide, globose, obtusely pentagonal, slightly carinate along the midrib of the upper half of the carpels, the sulci between the carpels extending a fifth to a third the way to the center of the fruit, hirsute-tomentulose, hairs stellate, forked and simple, 0.1–0.3 (–0.5) mm. long, the stipe 0–0.6 mm. long; dehiscence septicidal into cocci open along the ventral suture, sometimes also a third to half way along the dorsal suture; seeds 1.7–2.4 mm. long, 0.9–1.5 mm. wide, trigonal, brown, 1 per cell.

Flowering specimens collected in January, March, May to October, and December; fruiting ones, in March, June to October, and in December.

TYPE LOCALITY: Honda and Santanna, Tolima, Colombia, at 234–720 meters elevation, isotype cited below.

DISTRIBUTION: Western Venezuela, Colombia, Ecuador, Peru, and western Bolivia, on open, wooded hillsides, in moist copse, along roadsides, desert stream bottom, dry grassy mountains, loam clearing, in full sun or semishade, at 234–2,100 meters elevation.

VENEZUELA: ZULIA: Perija, *Gines* 2148 (US).

COLOMBIA: Valle del Magdalena, *Karsten* s.n. (W). MAGDALENA: Santa Marta, *H. H. Smith* 733 (A, K, L, US); Vista Nieve, Santa Marta, *Viereck* 9 (US). NORTE DE SANTANDER: REGIÓN DEL SARARE: Hoya del rio Chitagá, sobre La Cabuya, *Cuatrecasas et al.* 12198 (US). CUNDINAMARCA: On the río Bogotá in the vicinity of the bridge of San Antonio de Tena, *Cuatrecasas* 8280 (US). "Guayabetal" to Monte Redondo SE. of Quetame, *Pennell* 1753 (US), 1794 (US). Villeta, *Karsten* s.n. (W). Road between Villeta and Guaduas, *Ariste-Joseph*, July 1923 (US). El Colegio, *Ariste-Joseph* 1046 (US). Sasaima, *A. Marie* 21E (US). TOLIMA: Honda, *Bonpland* 1701 (P, isotype, presumably of *Mougeotia mollis* H.B.K.). *Andre* s.n. (K). F neg. 9606 ex B, *Humboldt & Bonpland*, presumably isotype of *Mougeotia mollis* H.B.K. (US). El Moral, Quindio, Mariquita, *Triana* (P, type of *Melochia globifera* Tr. & Pl., also US neg. 5663). "La Trinidad," Libano, *Pennell* 3249 (NY, US). TOLIMA?: La Vibora, Central Andes, *Lehmann* 4751 (US). HUILA: Cordillera Oriental, E. of Neiva,

Rusby & Pennell 445 (NY). ANTIOQUIA: Bello, *Bro. Thomas* 1011 (US); *Archer* 184 (US). VALLE DEL CAUCA: Rio Bolo, *Dryander* 752 (US). Rio Cali in the vicinity of Cali, *Ewan* 15853 (US). Quebrada Rio Yumbo, above Yumbo, *Ewan* 15839 (US). Espinal, below Dagua, *Killip & Hazen* 11063 (US). NARIÑO: Guaitara, *Karsten* s.n. (W). Pasto, *Karsten* s.n. (W).

ECUADOR: Eastern Cordillera, *Rimbach* 271 (US). TUNGURAHUA: Baños, *Tate* 623 (US).

PERU: In valleys of the Andes, *Haenke* s.n. (PR 174402 a, b, type of *Riedleia multiflora* Presl, also US neg. 5552). Pillao circa Chacahuassi, F. neg. 9603 ex B of *Ruiz*, collected in 1787 det.? HUÁNUCO: Cuchero, *Poeppig* 1269 in part (L, P, W). Near Cuchero, ?*Poeppig* 1379, September 1829 (W). Muña, *Macbride* 4005 (US) det.? JUNÍN: Huacapistana, *Sandeman* 4511 (K, also US neg. 5418), 4511A (K). San Ramón, *Killip & Smith* 24786 (W). AYACUCHO: Ccarrapa, between Huanta and Río Apurimac, *Killip & Smith* 22323 (US). CUSCO: CONVENCION: Hda. Sahuayaco, *Vargas C* 1685 (GH).

BOLIVIA: South Yungas, Sirupaya at Yanacachi, *Buchtien* 511 (US). Near Yungas, *Rusby* 1848 (NY, US).

This species is similar to *M. lupulina* Sw., but it is more robust, has longer and thicker peduncles and hairier stems and leaves, and the hairs are often brownish.

20. Melochia colombiana Cuatr. Rev. Acad. Colomb. Cienc. 8(32):486. 1952.

A branched, erect suffrutex at least 0.4 meter high, the young stems and petioles densely tomentose, hairs stellate 0.5–1.3 mm. long, light brown, internodes 0.4–0.7 cm. long; stipules 3.5–5.2 mm. long, 0.6–1.0 mm. wide, lanceolate, densely tomentose, hairs 0.3–1.0 mm. long; petiole 0.2–0.5 cm. long.

Lamina 1.1–3.8 cm. long, 0.7–2.0 cm. wide, ovate to nearly oval, the base rounded, the apex acute to slightly rounded, both surfaces densely tomentose, lanate, woolly to the touch, hairs tan, stellate and simple, 0.3–1.0 mm. long, the margin irregularly crenate-serrate, serrations 1–2.7 mm. wide, 0.5–2.0 mm. high, 8 or 9 pairs of primary veins, 2 are basal.

Inflorescences axillary, in upper 2–4 axils, 2.1–3.1 cm. long, the peduncle 1.2–1.6 cm. long, with branch 0.8 cm. long, the ultimate divisions umbellate, 5–10 flowers in a cluster, the pedicels 1.5–3.0 mm. long; bracts 1.5–3.0 mm. long, 0.2 mm. wide, lanceolate to nearly linear, densely tomentose, hairs 0.3–1.0 mm. long.

Calyx 5–5.7 mm. long, 4.8–5.3 mm. wide, not accrescent, densely tomentose on the outside, hairs stellate, 0.3–0.7 mm. long, the teeth 2.5 mm. long, 1.5–2.2 mm. wide, deltoid-acute, the sinus acute; petals yellow, 5 mm. long, 1.1–1.3 mm. wide, oblanceolate, the claw 0.5–0.6 mm. long, apparently free from the staminal tube.

Longistylous form not seen.

Brevistylous form. Stamens 4.5–4.9 mm. long, the filaments free for 1.5 mm., the anther 1.1–1.2 mm. long, 0.5–0.6 mm. wide, oblong, emarginate at both ends, nearly to the middle from the apex; pistil

3–3.5 mm. long, the styles filiform, stigmatic for 0.5 mm., 1.5 mm. long, free to the ovary, the ovary globose, densely tomentulose, hairs 0.3–0.5 mm. long.

Fruit 4 mm. long, 4.5 mm. wide, globose, pentagonal, the distal half of carpels somewhat carinate along the midrib, sometimes a slight hump about the middle of the dorsal surface of the carpels, the sulci extending a third to a fourth the way to the center of the fruit, densely tomentulose, hairs stellate, 0.3–0.6 mm. long, the stipe 0–0.3 mm. long; dehiscence septicidal into cocci open along the ventral suture, and sometimes a third along the dorsal suture; seeds 2.2–2.3 mm. long, 1.3 mm. wide, brown, 1 per cell.

Flowering and fruiting specimens collected in September.

TYPE LOCALITY: Colombia, Dept. del Valle, western slope of the Cordillera Occidental. Lobo Guerrero in xerophytic habitats, at 610–650 meters elevation. The type was collected by Cuatrecasas, no. 17804, and is cited below.

DISTRIBUTION: The species is known only from the type locality.

COLOMBIA: VALLE DEL CAUCA: CORDILLERA OCCIDENTAL: Lobo Guerrero, *Cuatrecasas* 17804 (F, type, also US neg. 5670).

This species is close to *Melochia mollis* (H.B.K.) Triana & Planch., but it has smaller laminae, shorter petioles, and shorter internodes.

21. Melochia leucantha Macb. Field Mus. Nat. Hist. Bot. Ser. vol. 13, pt. 3A No. 2:625. 1956.
PLATE 2

A branched, procumbent shrub 0.4–0.8 meter high, the young stems and petioles cinereous, tomentulose, hairs stellate, 0.1–0.3 mm. long, internodes 1–2.8 cm. long; stipules 2.8–6.0 mm. long, 0.7–1.5 mm. wide, deltoid-acuminate, tomentulose, hairs stellate, sometimes a few simple cilia, 0.1–0.7 mm. long; petiole 0.3–0.9 cm. long.

Lamina 1.7–4.0 cm. long, 1.0–3.2 cm. wide, broadly ovate, the base rounded to subcordate, the apex acute to rounded, velvety to the touch, the upper surface greenish-canescent-cinerous, tomentulose, hairs stellate, 0.1–0.3 (–0.4) mm. long, the lower surface canescent-cinereous, tomentulose, hairs stellate, 0.1–0.3 mm. long, the margin irregularly crenate-serrate, serrations 1.0–3.6 mm. wide, 0.3–1.8 mm. high, 5–9 pairs of primary veins, 2 or 3 are basal.

Inflorescences corymbiform to paniculate, the ultimate divisions umbellate, 3–10 flowers per umbel, in the axils of the upper 1–3 leaves, 2.5–6.5 cm. long, and terminal, extending 2.2–4.4 cm. beyond the first leaf, the peduncle 0.7–2.8 cm. long, the pedicels 1.5–3.0 mm. long; bracts 1–4.5 mm. long, 0.2–1.0 mm. wide, lanceolate to linear, tomentulose and sometimes ciliate, hairs stellate, 0.1–0.5 mm. long.

Calyx 5.9–6.3 mm. long, to 6.6 mm. long in the fruiting stage, 4.5–5.2 mm. wide, cinereous, densely tomentulose, hairs stellate, a few

forked, 0.1–0.5 mm. long, the teeth 3.1–4.0 mm. long, 1.5–2.3 mm. wide, deltoid-acuminate, the sinus acute; petals white, 6.8–7.2 mm. long, 2.0–2.8 mm. wide, obovate to nearly elliptic, cuneate, the claw 0.3–1.0 mm. long, free from the staminal tube or attached to it for 0.5 mm.

Longistylous form. Stamens 4.5–4.9 mm. long, the filaments united up to the anthers, the anther 1.4–1.6 mm. long, 0.8–0.9 mm. wide, oblong, emarginate at both ends, nearly to the middle from the apex; pistil 5.1–5.6 mm. long, the styles filiform, clavate and stigmatic at the apex for 0.7 mm., 3.1–3.4 mm. long, free to the ovary, the base of styles and ovary tomentulose, hairs stellate, few glandular, 0.1–0.2 mm. long, the ovary globose, pentagonal.

Brevistylous form. Stamens 5.5–6.0 mm. long, the filaments free for 2–2.3 mm., the base of staminal tube tomentulose for 1.3 mm. in tufts alternate with the filaments, hairs stellate 0.1–0.2 mm. long, the anther 1.2–1.4 mm. long, 0.5–0.6 mm. wide, oblong, slightly emarginate at both ends; pistil 3.7–4.2 mm. long, the styles filiform, papillose for 0.5–0.7 mm. at the apex, 2.1–2.5 mm. long, free to the ovary, the base of styles and ovary tomentulose, hairs stellate, 0.1–0.2 mm. long.

Fruit 3.8 mm. long, 3.9 mm. wide, globose, pentagonal, the angles somewhat acute, the sulci between the carpels extending a third of way to the center of the fruit, tomentulose, hairs mostly stellate, a few forked and simple, 0.1–0.3 mm. long, the stipe 0.5 mm. long; dehiscence septicidal into cocci open along the ventral suture; seeds not quite ripe, 2.4 mm. long, 1.5 mm. wide, trigonal, brown, 1 per cell.

Flowering and fruiting specimens collected in March.

TYPE LOCALITY: Eight kilometers east of Mejorada, Huancavelica, Peru, in gravelly shrublands at 2,400 meters elevation. The type is Goodspeed Expedition No. 10908, collected by Stork & Horton, cited below.

DISTRIBUTION: Common, though not abundant, in shrubland from Cusco, Peru, westward, at 2,000–2,400 meters elevation.

PERU: HUANCAVELICA: HUANCAVELICA: Eight km. E. of Mejorada, *Stork & Horton* 10908 (UC, type, also US neg. 5616). TAYSCAJA: Valley of the Mantaro River below Colcabamba, *Weberbauer* 6438 (GH, US). AYACUCHO: *Soukup* 4014 (US). Macbride (30) also reports the species from Río Pachuchaca, Apurímac, Peru.

This species is close to *M. mollis* (H.B.K.) Triana & Planch., but differs by having a loose corymbiform inflorescence, rather than subcapitate clusters; the leaves of *M. mollis* are covered with longer, often simple and forked as well as stellate hairs, that are brownish rather than cinereous-canescent.

22. Melochia lupulina Sw. Prodr. Veg. Ind. Occ. 97. 1788.
Mougeotia inflata H.B.K. Nov. Gen. & Sp. 5:330, *pl. 484.* 1823.
Riedleia inflata (H.B.K.) DC. Prodr. 1:491. 1824.
Visenia inflata (H.B.K.) Spreng. Syst. 3:30. 1826.
Visenia lupulina (Sw.) Spreng. Syst. 3:31. 1826.
Riedleia melissaefolia Presl, Rel. Haenk. 2:149. 1835.
Melochia inflata (H.B.K.) Benth. Bot. Voy. Sulph. 71. 1844.
Riedleia lupulina (Sw.) Beurl, Vet. Akad. Handl. Stockh. 115. 1854 (1856).
Anamorpha waltherioides Triana & Karst. *in* Triana, Neuv. Jen. i Esp. Fl. Neo-Granad. 10. 1854.
Physocodon macrobotrys Turcz. Bull. Nat. Mosc. 31(1):213. 1858.

An erect herb to trailing suffrutex, often with several slender stems from the base, 0.45–3.6 meters long, the young stems hirsute-tomentose, hairs stellate, forked, simple, and sometimes glandular, 0.2–2 mm. long, internodes 2.5–7.0 cm. long; stipules 3.4–6.0 mm. long, 0.3–1.3 mm. wide, deltoid-acuminate, mostly ciliate, hairs 0.1–1.0 mm. long; petiole 0.7–6.7 cm. long, tomentose, hairs 1–2 mm. long.

Lamina 3–11.8 cm. long, 1.5–8.5 cm. wide, ovate, the base rounded to cordate, the apex acute to subacuminate, the upper surface green, hairs mostly simple, appressed, not much overlapping, sometimes a few stellate and forked, 0.2–1.5 mm. long, more numerous on the lower surface, which is subtomentose, hairs simple, forked, stellate, and sometimes glandular, 0.3–1.5 mm. long, the margin irregularly crenate-serrate, serrations 1–3 mm. wide, 0.6–2.0 mm. high, 7–11 pairs of primary veins, 2 are basal.

Inflorescences axillary, umbellate, clusters at upper 4–16 nodes, usually 2 or 3 clusters per axil, 2–9 flowers in a cluster, the peduncle short and slender, 0.1–0.7 cm. long, 0.3–0.5 mm. wide, the pedicel 1–5 mm. long; bracts 1.5–4.0 mm. long, 0.1–0.7 mm. wide, deltoid-acuminate to sublinear, mostly ciliate, hairs 0.1–1.5 mm. long.

Calyx membranous, greenish white, at anthesis 5.0–5.6 mm. long, 4.5–5.5 mm. wide, accrescent, becoming 8–12.3 mm. long, 12 mm. wide, densely tomentulose, hairs stellate, forked, and sometimes glandular, 0.2–0.5 mm. long, the teeth at anthesis 2.5–3.2 mm. long, 1.7–2.3 mm. wide, becoming 4.3–6.5 mm. long, 3.6–4.6 mm. wide, deltoid-acute to deltoid-acuminate, the sinus acute; petals usually white, sometimes yellowish white or white distally and yellow proximally, 4.5–7.2 mm. long, 1.6–2.1 mm. wide, obovate or oblanceolate, the blade rather sharply demarcated from the claw, claw 0.5–0.7 mm. long, apparently not attached to the staminal tube.

Longistylous form. Stamens 3.3–4.0 mm. long, the filaments united up to the anthers, the anther 1.0–1.2 mm. long, 0.6 mm. wide, emarginate at both ends, nearly to the middle from the apex, sacs divergent at the apex; pistil 4.5–5.8 mm. long, the styles 3.2–4.2 mm. long, free to the ovary, tomentose at the base, papillose at the apex

for 0.9 mm., the ovary subglobose, shallowly pentagonal, tomentulose, hairs 0.1 mm. long, the stipe 0.5 mm. long.

Brevistylous form. Stamens 4.2 mm. long, the filaments free for 2 mm., the anther 0.9–1.2 mm. long, 0.5–0.7 mm. wide; pistil occasionally of 6 carpels, 2.5 mm. long, the styles 1.5 mm. long, free to the ovary, papillose for 0.5 mm.

Fruit 2.5–3.2 mm. long, 2.9–4.3 mm. wide, globose, pentagonal, the sulci shallow, the cocci compressed, carinate, tomentulose, sometimes also glandular, hairs 0.1 mm. long, the stipe 0.5–0.7 mm. long; dehiscence septicidal into cocci, open along the ventral suture; seeds 1.7–2.2 mm. long, 1.1–1.3 mm. wide, trigonal, the sides flat, the dorsum rounded, brown.

Flowering and fruiting specimens collected throughout the year, but flowering most commonly from October to February.

TYPE LOCALITY: The type was collected by Swartz in Jamaica and is cited below.

DISTRIBUTION: Mexico, Central America, Jamaica, Venezuela, Colombia, Ecuador, and Peru, usually in moist thickets on shaded river banks, also in llanos, campo, savannas, and weedy fields, in loam or clay soil, at 0–3,150 meters elevation.

MEXICO: "In the land of western Mexico," *Haenke* (PR 174401 a, b, type of *Riedleia melissaefolia Presl*, also US neg. 5551). CHIAPAS: Vol. Tacana, Union, *Matuda* 2788 (MICH).

GUATEMALA: ALTA VERAPAS: *von Türckheim* II 2201 (US). Finca Mocca, *H. Johnson* 86 (US). Chicacoa, *J. D. Smith* 1764 (US). Near the Finca Sepacuite, *Cook & Griggs* 292 (US). Between Cahabon and Secanquim, *Goll* 129 (US).

BRITISH HONDURAS: El Cayo District, *Bartlett* 12888 (MICH, S), 11426 (MICH). El Cayo and vicinity, *Chanek* 206 (MICH). Vaca, *Gentle* 2267 (MICH).

HONDURAS: YORO: Quebrada Seca, *Standley* 53896 (US). EL PARAÍSO: Quebrada del Ingenio de los Angeles, *Standley* 29417 (US).

COSTA RICA: ?Salamanca, *Tonduz* 8613 (US). Between Barba and Santa Barbara, *Pittier* 1684 (US). Santiago, *Stork* 1246 (MICH). ?ALAJUELA: Alajuelita, *Tonduz* 1479 (US). SAN JOSÉ: Between Aserri and Tarbaca, *Standley* 34054 (US), 41343 (US). Las Vueltas, Tucurrique, *Tonduz* 12871 (GH, US, W). Vicinity of San José, *Tonduz* 10901 (US). Vicinity of El General, *Skutch* 2269 (S, US). CARTAGO: Vicinity of Pejivalle, *Standley & Valerio* 46802 (US). Rio Turrialba, *J. D. Smith* 6456 (US).

PANAMA: Porto-Bello, *Billberg* 292 (S). *Andersson* s.n. (S). Almerante, *Skutch* (US). Changuinola Valley along R. R., *Dunlap* 334 (US). Nature trail at Camp No. 1 on Madden Dam Highway, *Elmore* 58 (MICH). BOCAS DEL TORO: *Carleton* 183 (US). Water Valley vicinity of Chiriqui Lagoon, *von Wedel* 1671 (US), 1848 (US). CANAL ZONE: Gamboa, *Standley* 28329 (US), 28501 (US). Vicinity of Summit, *Standley* 25817 (US), 26932 (US), 29630 (US), 30059 (US). Hills W. of the Canal, near Gatún, *Standley* 27273 (S, US). Gatún, *Bro. Heriberto* 22 (US). Frijoles, *Standley* 27640 (US). Darien Station, *Standley* 31524 (US). Obispo, *Standley* 31772 (US). Empire to Mandinga, *Piper*

5460 (US). Pedro Miguel, *Piper* 5498 (US). Rio Grande, near Culebra, *Pittier* 2109 (US). Vicinity of Monkey Hill, *Cowell* 39 (US). PANAMÁ: N. of Panama City, *Bro. Paul* 613 (MICH). Rio Tapia, *Standley* 28053 (US). Between Matías Hernández and Juan Díaz, *Standley* 32063 (US). Matías Hernández, *Pittier* 6900 (US). DARIÉN: Along Sambú River, *Pittier* 5537 (US).

JAMAICA: *Swartz* s.n. (S, type, also US neg. 5615). Kempshot, *Harris* 10328 (US). Near Holland Bay, St. Thomas, *Harris* 11955 (S, US). Phillipsfield near Bowden, *Harris & Britton* 10783 (US). Along trail from Bath to Cuna Cuna Pass, *Maxon* 1691 (US). Sulphur River, near the Fountain, 1 mi. N. of Bath, *Mrs. K. L. Hart* s.n. (IJ). Cedar Valley, *Mrs. K. L. Hart* s.n. (IJ). Between Whitehall and Big Hill, *Proctor* 7674 (IJ). Gorge of Plantain Garden River NNW. of Whitehall, St. Thomas, *Proctor* 11783 (IJ); *Stearn* 485 (S).

VENEZUELA: MIRANDA: Las Mostazas on R.R. beyond Los Teques, *Allart* 206 (US), 285 (US). (These two specimens lead toward *M. mollis* [H.B.K.] Triana & Planch.)

COLOMBIA: *Dawe* 851 (US). BOLÍVAR: Rio Sinú, Cartagena, *Humboldt & Bonpland* 1369 (P, isotype of *Mougeotia inflata* H.B.K., F. neg. 35380 ex P [US], also US neg. 5660). Sincelejo, *Pennell* 4074 (US). Occidente de Monteria, near Rio Sinú, *Cervantes, Molina & Barkley* 19 Bo 053 (US). SANTANDER: Vicinity of Barranca Bermeja, Magdalena Valley, *Haught* 1533 (US). CUNDINAMARCA: Route de Villavicencio, Guyabetal, *Humbert et al.* 27146 (P, US). ANTIOQUIA: Vicinity of Medellín, *Barkley* 18 C 663 (US). CALDAS: Salamina, *Bro. Daniel* 2785 (US). VALLE DEL CAUCA: Guanabanal, *Killip* 6222 (US). "Potredillo" to "Miraflores," Palmira, *Pennell & Killip* 6063 (US). Cisneros, *Killip* 5368 (US), 35521 (US). CAUCA: *Karsten* s.n. (W, ?isotype of *Anamorpha walltherioides* Triana & Karst.). Piedra de Moler et Cartago, *Triana* s.n. (P, ?type of *Anamorpha walltherioides* Triana & Karst., also US neg. 5662).

EQUADOR: Balao, *Eggers* 14066 (L, US). Terecita, *Stevens* 143 (US). 21 km. SW. of Guayaquil, *Worth et al.* 8933 (US). Vicinity of Portovelo, *J. N. & G. Rose* 23438 (US). 8 km. N. of Guayaquil, *Stork et al.* 8974 (US). GUAYAS: Chongón, *Asplund* 5860 (R), 7683 (US). Rio Grande near Hacienda Tenguel, *Holmgren* 30 (S, US). Guayaquil and vicinity *Fagerlind & Wibom* 105 bis (S); *Hitchcock* 19934 (US); *Hartweg* 643 (W); *Jameson* 361 (LE, also US neg. 5270, isotype of *Physocodon macrobotrys* Turcz.). Oil camp between Guayaquil and Salinas, *Hitchcock* 20044 (US). Milagro, *Hitchcock* 20191 (US). Daule, *Fagerlind & Wibom* 371 (S). Near a tributary of Rio Daule 1.5° S. lat., *Boecher et al.* 39 (S). Los RIOS: Near Quevedo, Canton Vinces, *Mexia* s.n. (US). CHIMBORAZO: Cañon of the Rio Chanchan near Huigra, *Camp* E–2943 (US). CAÑAR: Valley of Rio de Cañar near Rosario, *Prieto* CP–21 (NY). EL ORO: Near junction of Rio Luis and Rio Ambocas, 10 km. S. of Portovelo, *Wiggins* 10892 (US).

PERU: *Haenke* s.n. (PR). SAN MARTÍN: Pucayacu 11 km. S. of Tarapoto, *Ferreyra* 7759 (US). LORETO: MAYNAS: Near Yurimaguas, *Poeppig* 2425 (P, W). Near Yurimaguas, at the River Huallaga, *Spruce* 3898 (W). LIBERTAD: Trujillo, *Killip & Smith* 21501 (US). Chicama Valley, *Smyth* 80 (US). LIMA: Lima and vicinity, *Savatier* 1658 (K), 1659 (K); *Née* s.n. (US); *Mathews* 1054 (W). Callao, insula S. Lorenzo, *Andersson*, Mar. 18, 1852 (S, US). Santa Clara, *Mr. & Mrs. J. N. Rose* 18735 (NY, US). Chosica, *Soukup* 1840 (US); *Macbride & Featherstone* 496 (US, W); *Asplund* 10897 (US). Ricardo Palma, *Reitz* 6016 (US). CHANCAY: Hda. Ana María, *Ferreyra* 7174 (US). HUÁNUCO: 15 mi. SE. of Huánuco, *Macbride & Featherstone* 2060 (US). JUNÍN: Colonia Perene, *Killip & Smith* 25064 (US).

Melochia lupulina Sw. can be distinguished from most members of the section *Mougeotia* by its markedly accrescent calyx. *Melochia mollis* (H.B.K.) Triana & Planch. may also have a markedly accrescent calyx, but it is more robust and usually taller than *M. lupulina*, 0.5–5 versus 0.45–3.6 meters high; *M. mollis* has longer and thicker peduncles, 0.5–8.0 cm. versus 0.1–0.7 cm. long, and it has hairier stems and leaves.

23. Melochia thymifolia (Presl) A. Goldberg, comb. nov. PLATE 3

Riedleia thymifolia Presl, Rel. Haenk. 2:149. 1835.

Melochia nervosa (should be *venosa*) Sw. *α typica* Schum. var. *purpurea* O. Ktze. Rev. Gen. 3(2):25. 1898.

Melochia yungasensis Rusby, Bull. New York Bot. Gard. 4:331. 1907.

Melochia pseudonodiflora Hochr. Ann. Cons. Jard. Genève 21:430. 1920.

A branched erect or decumbent subshrub 0.2–0.9 meter high, sometimes with numerous (to 10) slender stems from the base, the taproot woody, thicker than the stem, 0.4–0.8 cm. wide, sometimes with secondary branches, the young stems and petioles tomentulose, canescent, hairs stellate, simple and forked, sometimes also glandular, 0.1–0.2 (–2.0) mm. long, internodes 0.5–5.0 cm. long; stipules 2.1–6.0 mm. long, 0.5–1.8 mm. wide, lanceolate or deltoid-acute or deltoid-acuminate, ciliate, hirsute or tomentulose, hairs simple, forked, stellate, and sometimes glandular, 0.1–0.2 (–1.5) mm. long, petiole 0.2–1.6 (–3.1) cm. long.

Lamina (0.9–) 1.5–4.5 (–7.5) cm. long, (0.5–) 1.3–3.0 (–4.5) cm. wide, usually broadly to narrowly ovate, sometimes oblong-ovate, the base usually rounded, sometimes subcordate or truncate, the apex acute to rounded, the upper surface green, with slightly overlapping, simple, appressed hairs, or sericeous-tomentose, a few hairs stellate and forked, sometimes also glandular, or only stellate and forked, 0.1–0.2 (—1.5) mm. long, the lower surface lighter green, with scattered hairs or tomentulose and slightly canescent, hairs mostly stellate, some forked, usually also simple, sometimes also glandular, 0.1–0.2 (—1.0) mm. long, velvety or slightly scabrous to the touch, the margin irregularly crenate-serrate, serrations 0.7–3.7 (–6.9) mm. wide, 0.4–2.0 (–3.1) mm. high, (4–) 5–9 pairs of primary veins, (1–) 2 are basal.

Inflorescences on axillary branches 0.7–9.5 cm. long, leafless or with reduced leaves, the flowers at 1–4 nodes, in the axils of the upper 1–6 (–9) leaves of the main stem and 1–3 leaves of the branches, also terminal, extending 1–6 cm. beyond the first leaf, racemose, corymbiform or spicate, the ultimate divisions subcapitate umbels of (1–) 3–5 (–10) flowers, peduncles absent, especially from the inflorescences of the branches, or 0.2–4.0 cm. long, slender 0.4–0.7 mm. wide, the

pedicel 0.5–3.0 (–4.0) mm. long; bracts 1.0–5.5 mm. long, 0.2–1.1 mm. wide, linear, lanceolate, lanceolate-ovate, or deltoid-acute, ciliate and hirsute or tomentulose, hairs simple, forked, and stellate, 0.1–0.6 (–1.5) mm. long.

Calyx sometimes reddish or purplish in the fruiting stage, (3.5–) 4.0–4.9 (–6.0) mm. long, 3.0–5.2 mm. wide, sometimes slightly accrescent, becoming 4.5–6.8 mm. long and 4.8–5.7 mm. wide, the external surface with scattered hairs or tomentulose, hairs simple, forked, and stellate, sometimes predominantly glandular or only stellate, minutely canescent at the apex of the internal surface, hairs 0.1–0.3 (–1.0) mm. long, the teeth (1.5–) 2.2–2.9 (–4.0) mm. long, 1.2–2.0 (–2.9) mm. wide, deltoid- to ovate-acute or slightly ovate-acuminate, the sinus usually acute, sometimes rounded; petals rose or purple, sometimes white, 4.2–7.5 mm. long, 1.5–2.7 mm. wide, obovate, elliptic-oblong, or oblanceolate, cuneate, free from the stamens, the claw 0.3–1.2 mm. long.

Longistylous form. Stamens 2.4–3.5 mm. long, the filaments united up to the anthers, the anther 0.8–1.1 mm. long, 0.5–0.8 mm. wide, oblong, emarginate at both ends, nearly to the middle from the apex, sacs divergent at the apex; pistil 2.6–5.8 mm. long, the styles 1.3–3.4 mm. long, free to the ovary, papillose for 0.7–0.8 mm. at the apex, the ovary globular-ovoid, pentagonal, densely sericeous, hairs 0.1–0.8 mm. long.

Brevistylous form. Stamens 4.1–5.1 mm. long, the filaments free for 2.0–2.3 mm., the anther 0.8–1.1 mm. long, 0.5–0.6 mm. wide, shape same as that above; pistil 2.3–2.6 mm. long, the styles 1.3–1.7 mm. long, free to the ovary, the ovary globular, tomentulose-sericeous, or only hirsute at the apex, hairs 0.1–0.3 mm. long.

Fruit 2.6–4.5 mm. long, 3.0–4.5 mm. wide, globular, pentagonal, the carpels narrowing toward the apex, middorsal surface of carpels rounded at the base, keeled in the upper half, the sulci between the carpels extending one-fourth (one-fifth at the middle and one-third at the apex) of way to the center of the fruit, with scattered hairs or tomentulose, hairs simple, forked, and stellate, sometimes also glandular, 0.1–0.5 mm. long, the stipe 0–0.4 mm. long; dehiscence septicidal into cocci open along the ventral suture, and sometimes readily separated for a fourth to half way along the dorsal suture; seeds trigonal, 1.8–2.6 mm. long, 1.1–1.7 mm. wide, rarely the testa of the chalazal end is loosened for 0.1–0.2 mm. and almost winglike, brown, 1 per cell.

Flowering specimens collected in February, April, June, August, September, and November; fruiting ones, in June, September, and November.

TYPE LOCALITY: The lectotype was collected by Haenke, PR 174403a, in Huánuco, Peru, and is cited below.

DISTRIBUTION: In the Andes of Ecuador to Bolivia, on open hillside, on schistose rocks or red, sandy soil, usually at 2,400–2,700 meters elevation, but extending downward toward the Amazon basin.

ECUADOR: CHIMBORAZO: Vicinity of Huigra, mostly on the Hda. de Licay, *J. N. & G. Rose* 22546 (GH).

PERU: "Peru et Chili," *Ruiz* s.n. (G, type of *Melochia pseudonodiflora* Hochr., also US neg. 5416). CAJAMARCA: Tambillo, *de Jelski* 282 (W, also US neg. 5546). AMAZONAS: Chachapoyas, *Mathews* 2115 (K), 3233 (K). HUÁNUCO: F neg. 9602 ex B of Ruiz, collected 1787 (US). "Peruvian Andes at Huanocco," *Haenke* (PR 174403 a and b, lectotype and isotype, respectively, also US neg. 5553). AMBO: Arriba de Quicacan, *Ferreyra* 6631 (US). JUNÍN: Carpapata, above Huacapistana, *Killip & Smith* 24331 (US).

BOLIVIA: Yungas, *Bang* 1977 (NY, type; US, isotype of *Melochia yungasensis* Rusby). LA PAZ: *Bang* 2132 (GH). Cotaña at Illimani, *Buchtien* 254 (GH, NY), 3222 (NY, S, US). LARECAJA: Vicinity of Sorata, *Mandon* 819 (K, S, US). COCHABAMBA: Tunari, *Kuntze*, April 1892 (NY).

This species is close to *Melochia nodiflora* Sw., but the young stems and leaves are generally hairier; the number of nodes with inflorescences are fewer, 1–6 (–9) versus up to 20; a peduncle is often present, it is usually absent in *M. nodiflora*, and shorter when present; the pedicels are generally slightly longer, the terminal inflorescence is more frequent and longer, and the sulci between the carpels are shallower than in *M. nodiflora*.

This species is also related to *Melochia nudiflora* Standl. & L. Wms., but the leaves have fewer primary veins, 5–9 versus 9–14. The bracts are narrow, to 1.1 mm. wide, in *M. nudiflora* the majority are broad, to 3.9 mm. wide. The petals are free of the staminal tube but attached to it for 1–2 mm. in *M. nudiflora*.

This species is also close to *Melochia lupulina* Sw., but the calyx is not accrescent or slightly so, becoming 4.5–6.8 mm. long and 4.8–5.7 mm. wide, in *M. lupulina* it becomes 8–12.3 mm. long and 12 mm. wide. There is only one flower cluster per axil, frequently 2 or 3 in *M. lupulina*. The pedicels are generally shorter and the peduncle, when present, is usually longer than in *M. lupulina*.

24. Melochia bernoulliana Donn. Smith, Bot. Gaz. 35:2. 1903.

A branched, slender shrub 1–4 meters high, the young stems and petioles covered with stellate hairs less than 0.1 mm. long, internodes 2–6 cm. long; stipules deciduous, 3.5–5.0 mm. long, 0.6–0.8 mm. wide, lanceolate, with silky hairs up to 0.3 mm. long; petiole slender, 0.3–3.6 cm. long.

Lamina thin, 3–11.5 (–13) cm. long, 1.1–7.5 cm. wide, usually ovate, sometimes also lanceolate, the base usually rounded, some-

times truncate or subcordate, the apex usually acuminate, sometimes acute, the upper surface of young leaves with appressed, simple, deciduous hairs 0.1–0.5 mm. long on the blade, and stellate hairs less than 0.1 mm. long on the veins, the lower surface with stellate hairs less than 0.1 mm. long on the veins, the margin irregularly crenate-serrate, serrations high, 1–5 mm. wide, 0.5–3.5 mm. high, 7–11 pairs of primary veins, 2 are basal.

Inflorescence slender, somewhat paniculate, the ultimate divisions usually umbellate, 2–5 flowers per umbel, the terminal inflorescence extending 3–5 cm. beyond the first leaf, the axillary inflorescences 2–13 cm. long, in upper 5–10 axils, slender axillary flowering branches 9–13 cm. long, the peduncle 0–2.0 cm. long, very slender, the pedicels relatively long, slender, 3–7 mm. long; bracts 1–3.7 mm. long, 0.2–1.5 mm. wide, ovate to nearly linear, with simple, forked, and stellate hairs 0.1–0.4 mm. long.

Calyx 3.5–5.0 mm. long, 4–6.5 mm. wide, not accrescent, covered with stellate, simple and glandular hairs up to 0.1 mm. long, the teeth 2.1–3.8 mm. long, 1.4–2.2 mm. wide, deltoid- to ovate-acute to ovate-acuminate, the sinus acute to narrowly rounded; petals pink with white at the tips, or purple, 5–7.3 mm. long, 2.2–2.9 mm. wide, obovate to oblanceolate, attached to staminal tube for 1 mm., the claw 0–0.5 mm. long.

Longistylous form. Stamens 3.4 mm. long, the filaments united up to the anthers, the anther 1.0–1.1 mm. long, 0.7 mm. wide, oblong, emarginate at both ends, almost to the middle from the apex; pistil 4.8–5.0 mm. long, the styles 3.5–3.7 mm. long, free to the ovary, papillose at the apex for 0.8–1.0 mm., the ovary ovoid, hirsute-sericeous, hairs 0.5 mm. long, stipe none.

Brevistylous form. Stamens 2.8–4.0 mm. long, the filaments free for 1.3–2.7 mm., filamentous staminodes 0.4 mm. long sometimes present; pistil 2.7–3.1 mm. long, the styles 1.3–1.6 mm. long, free to the ovary, the ovary ovoid, hirsute, hairs forked, 0.3–0.5 mm. long.

Fruit obtusely pentagonal, depressed-globose, 3.5–4.1 mm. long, 4.4–4.8 mm. wide, with forked and simple hairs 0.1–0.5 mm. long and stellate hairs less than 0.1 mm. long, deeply sulcate between the carpels, the sulci extending half way to the center of the fruit, stipe none; dehiscence septicidal into cocci open along the ventral suture; seeds 2.1–2.4 mm. long, 1.4–1.6 mm. wide, red brown.

Flowering and fruiting specimens collected from October to December (old fruit sometimes still present in March).

TYPE LOCALITY: Retalhuleu (Bernoulli & Cario 3112) and Santa Rosa (Heyde & Lux 4319), Guatemala; lectotype and paratype cited below.

DISTRIBUTION: Chiapas, Mexico, to San Vicente, Salvador, in moist or dry thickets, sometimes on cliffs or along streams, at 350–800 meters elevation.

MEXICO: CHIAPAS: Escuintla, *Matuda* 485 (MICH, US), 2129 (MICH). GUATEMALA: RETALHULEU: *Bernoulli & Cario* 3112 (S, paratype). SANTA ROSA: Mouth of the Rio De Los Esclavos, *Heyde & Lux* 4319 (US, lectotype). SALVADOR: SONSONATE: Near headwaters of Rio Acachapa, Hda. Las Tablos, Balsam Range, *Tucker* 1324 (US). LA LIBERTAD: Ateos, *Calderón* 1858 (GH, US). SAN VICENTE: Vicinity of San Vicente, *Standley* 21676 (US).

This species is characterized by its slender, open, somewhat paniculate inflorescences, long slender pedicels, and thin lamina with very short pubescence and high serrations. It is perhaps most closely related to *Melochia lupulina* Sw. but does not have an accrescent calyx.

25. Melochia nodiflora Sw. Prodr. Veg. Ind. Occ. 97. 1788.
Melochia carpinifolia Wendl. Bot. Beobacht. 52. 1798.
Mougeotia nodiflora (Sw.) H.B.K. Nov. Gen. & Sp. 5:330. 1823.
Riedleia nodiflora (Sw.) DC. Prodr. 1:491. 1824.
Visenia nodiflora (Sw.) Spreng. Syst. 3:30. 1826.
Riedleja urticaefolia Turcz. Bull. Soc. Nat. Mosc. 31(1):209. 1858.
Melochia conglobata Sessé & Moc. Pl. Nov. Hispan. ed. I, 106. 1889.
Melochia urticaefolia (Turcz.) Standl. Contr. U.S. Nat. Herb. 23:804. 1923.

An erect or spreading herb to slender, branched shrub 0.5–4.0 meters high, the taproot somewhat thicker than the stem, the young stems puberulous, hairs simple and forked, 0.1–0.2 (–0.6) mm. long, internodes 1.3–3.2 cm. long; stipules soon deciduous, 1.7–5.2 mm. long, 0.7–2.9 mm. wide, deltoid- to ovate-acute, hirsute-ciliate, hairs scattered, appressed, 0.2–0.8 mm. long; petiole 0.6–4.3 cm. long, hirsute-tomentose, hairs simple and forked, 0.4–1.0 mm. long.

Lamina 3.5–7.5 (2–11.9) cm. long, 1.5–5.3 (1.0–7.7) cm. wide, usually ovate, sometimes also ovate-lanceolate, the base rounded to cordate, or subtruncate, the apex acute, the upper surface green, subglabrate, a few scattered, simple, appressed hairs 0.1–0.7 mm. long, the lower surface green, subglabrate or puberulous, a few scattered simple, rarely also forked and stellate hairs, appressed or erect, 0.1–0.7 mm. long, the margin irregularly crenate-serrate, serrations 1.5–4.8 mm. wide, 0.7–2.0 mm. high, 7–10 pairs of primary veins, usually 2 are basal, the second pair thicker than the first.

Inflorescences axillary, in heads of 2–10 flowers at the upper 15–20 nodes, peduncle usually none, rarely 0.4–0.6 cm. long, sometimes naked axillary branches up to 7.5 cm. long with flowers at several nodes, the pedicel 0–2 (–3) mm. long; bracts 1.7–3.0 mm. long, 0.2–1.1 mm. wide, rarely wider and 2 united, deltoid-acute to deltoid-

acuminate or nearly linear, hirsute-ciliate, hairs simple, 0.3–0.7 mm. long.

Calyx sometimes dull red in the fruiting stage, 3.2–7.0 mm. long, 3–3.8 mm. wide, not accrescent, hirsute-ciliate, hairs simple and forked, 0.1–1.0 mm. long, the teeth 2–3 mm. long, 0.5–1.5 mm. wide, deltoid-acute to deltoid-acuminate or ovate-acuminate, the sinus acute; petals most commonly pink, also purplish, white with red or pink veins, pale pink with purplish-red veins, white, rarely yellow, 3.7–4.9 (–7.0) mm. long, 1.4–2.1 mm. wide, obovate, oval or elliptic, the claw 0–0.5 mm. long, base of petals shortly and loosely united to the staminal tube.

Longistylous form. Stamens 2.7–3.0 mm. long, the filaments united up to the anthers, the anther 0.7–0.9 mm. long, 0.4–0.6 mm. wide, oblong, emarginate at both ends, nearly to the middle from the apex, sacs slightly divergent at the apex; pistil 3.2–3.5 mm. long, the styles 1.3–2.0 mm. long, free to the ovary, papillose at the apex for 0.5 mm., the ovary ovoid or orbicular, hirsute, hairs simple, to 0.5 mm. long.

Brevistylous form not seen.

Fruit rarely of 6 carpels, 3.0–3.5 mm. long, 3.9–4.5 mm. wide, oblate-spheroid, pentagonal, the sulci between the carpels extending half way to the center of the fruit, hirsute, hairs simple, 0.4–1.0 mm. long, stipe none; dehiscence septicidal into cocci open along the ventral suture; seeds 2–2.2 mm. long, 1.1–1.4 mm. wide, trigonal, brown or tan.

Flowering specimens collected from August to April; fruiting ones, from July to May, both most commonly from November to February in the Northern Hemisphere.

TYPE LOCALITY: The type was collected by Swartz in Jamaica and is cited below.

DISTRIBUTION: Mexico to northern and eastern Brazil and the West Indies, in moist thickets, along the roadside, in cultivated ground, in waste ground, in sandy or open woods, in pastures, in wet or dry places on rocky, calcareous or sandy soil, at 0–1,800 meters elevation.

MEXICO: *Sessé et al.* (MA, type of *Melochia conglobata* Sessé & Moc.). **F** neg. 30510 ex MA of drawing of *M. congloblata* Sessé & Moc. (F). SINALOA: Imala, *Gentry* 4968 (GH). JALISCO: San Sebastian, Sierra Madre Mts., *Mexia* 1475 (A). VERA CRUZ: *Orcutt* 3168 (K, US). Zacuapan, Barranca de Santa Maria, *Purpus* 2358 (US). Rio de la Ternera, *Purpus* 8276 (US). Santa Lucrecia, *Mell* 667 (US). Cameron, *Purpus* 8630 (UC). MEXICO: TEMASCALTEPEC: *Hinton* 2072 (US). Chorrera, *Hinton* 5368 (US). Peñón, *Hinton* 2144 (US). Ixtapan, *Hinton* 2950 (MICH, S). MICHOACÁN: ZITÁCUARO: Zitácuaro-La Florida, *Hinton* 13407 (MICH, US). W. of Jiquilpan along highway to Colima, *McVaugh* 13207 (MICH, US). GUERRERO: Acapulco and vicinity, *E. Palmer* 261 in part (MICH, US). COYUCA: Coyuca-Chacamerito, *Hinton* 5689 (US). MINA: Manchon, *Hinton* 9640 (K, US). GALEANA: Plan de Carrizo,

Hinton 11024 (US). Oaxaca: *Galeotti* 4091 (W, isotype of *Riedleja urticaefolia* Turcz., also US neg. 5547). Vicinity of Cafetal Concordia, *Morton & Makrinius* 2706 (US), 2321 (US). Pochutla, *Conzatti et al.* 3021 (US), 3193 (US). YUCATAN: Izamal, *Gaumer* 948 (US). Chichankanab, *Gaumer* 2080 (MICH, US). Xnoćać, *Gaumer & sons* 23507 (S, US).

GUATEMALA: *Hyde* 631 (US). Gualan, *Deam* 267 (MICH). SANTA ROSA: Volcan Jumaytepeque, *Heyde & Lux* 4317 (US).

BRITISH HONDURAS: Prospecto, Northern River, *Gentle* 922 (MICH). Little Cocquericot, Belize River, *Lundell* 4235 (MICH).

HONDURAS: Vicinity of Amapala, Isla Tigre, *Standley* 20696 (US).

SALVADOR: Cerro del Guayabal, *Calderón* 1958 (US). Zacatecoluca, *Calderón* 329 (US). AHUACHAPÁN: *Padilla* 473 (US). Vicinity of Ahuachapán, *Standley* 20216 (US). SAN VICENTE: Volcán de San Vicente, *Iglesias* 1 (US). SAN MIGUEL: Hacienda San Antonio, *Calderón* 2121 (US). MORAZÁN: Easternmost peak, Montes de Cacaquatique, near summit on N. side, *Tucker* 630 (US). LA UNION: *Grant* 720 (MICH).

NICARAGUA: *C. Wright* s.n. (US). Granada, *Baker* 582 (US). Ometepe Island, Lake Nicaragua, *Shimek & C. L. Smith* 110 (US). MANAGUA: *Chaves* 31 (US). CHONTALES: *Friedrichsthal* 725 (W).

COSTA RICA: Around Nicoya, *Tonduz* 13489 (GH, US). Near Río Terraba, vicinity of Palmar Norte de Osa, *Allen* 5451 (MICH). GUANACASTE: Vicinity of Libano, *Standley & Valerio* 44906 (US). Vicinity of Tilarán, *Standley & Valerio* 45690 (US). Bebedero, *Standley & Valerio* 46685 (US).

PANAMA: *Seemann* 473 (S). Pearl Islands, *Johansen* 116 (US). Isthmus of Panama, *Hayes* 154 (GH). CHIRIQUÍ: Vicinity of San Carlos, *Allen* 1140 (US). CANAL ZONE: Balboa, *Standley* 25545 (US), 27126 (US), 29260 (US), 32112 (US). Near Summit, *Standley* 29649 (US). Vicinity of Miraflores Lake, *White* 260 (US). Along the old Las Cruces Trail, between Fort Clayton and Corozal, *Standley* 29149 (US). PANAMA: Vicinity of Panama, *Macbride* 2618 (US). Vicinity of Matías Hernández, *Standley* 28870 (US); *Pittier* 6905 (US). Between Matías Hernández and Juan Díaz, *Standley* 32092 (US). Between Las Sabanas and Matías Hernández, *Standley* 31847 (US). Bella Vista, *Standley* 25307 (S, US). Near Chepo, *Hunter & Allen* 61 (S).

BAHAMAS: NEW PROVIDENCE: Nassau, *Curtiss* 26 (L, US); *Britton & Millspaugh* 2087 (US).

CUBA: *C. Wright* 39 (US). *de la Sagra* 69 (W). *Merat* s.n. (W). Yumuny, *Rugel* 27 (L). Tumbadero, *Otto* 77 (W). PINAR DEL RÍO: Sierra de Anafe, *Wilson* 11490 (US). HABANA: Anafe near Lago de Ariguanabo, *Ekman* 1041 (S). Santiago de las Vegas, *Wilson* 3642 (UC, US). LAS VILLAS: Limones, Soledad, Cienfuegos, *Pringle* 84 (R, US); *Jack* 4622 (US), 6649 (S), 6895 (S, US). CAMAGUEY: Vicinity of La Gloria, *Shafer* 46 (US). ORIENTE: Vicinity of Baracoa, *Pollard et al.* 12 (US). Baracoa, at margin of Rio Toa, *Ekman* 4063 (S). Santiago de Cuba, *Ekman* 8467 (S), 8988 (S). Bayate, *Ekman* 4534 (S).

HAITI: Port-au-Prince, *Eggers* 3312 (S); *Holdridge* 1027 (MICH, US); *Leonard* 2801 (US). Vicinity of Port de Paix, ridge W. of La Coup River, *E. C. & G. M. Leonard* 11128 (US). Massif de la Hotte, Fond-des-Nègres, *Ekman* H7200 (S, US). Vicinity of Jean Rabel, *E. C. & G. M. Leonard* 12805 (US), 12632 (US). Dept. du Nord, vicinity of Plaisance, *Leonard* 9247 (US), 9286 (US). Vicinity of St. Michel de l'Atalaye, *Leonard* 7077 (US), 7729 (US), 8019 (US). Morne de l'Hôpital, ?*Ticanda* 1202 (S). Vicinity of St. Louis du Nord, *E. C. & G. M. Leonard* 14176 (US).

DOMINICAN REPUBLIC: *C. Wright et al.* 105 (US). *von Türckheim* 2579 (L, S, US). San Pedro de Macoris, *Rose et al.* 3713 (US). Azua, *Rose et al.*

4057 (US). SANTO DOMINGO: Vicinity of Ciudad Trujillo, *Allard* 13378 (US), 13400 (S, US), 13688 (US), 13696 (US), 14622 (US). Santo Domingo City, *Ekman* 10941 (S, US). BARAHONA: Riocito, *Fuertes* 199 (US).

JAMAICA: *Swartz* s.n. (S, type, also US neg. 5608). Upper slopes of Mount Diablo, *Maxon & Killip* 423 (US). Spanish Town, *Clute* 36 (US). Near Ewarton, *Harris* 6615 (US). Above Kingston, *Lehmann* B. T. 896 (L). GRAND CAYMAN: *Proctor* 9565 (IJ).

PUERTO RICO: *Krebs* s.n. (S). Sabana Grande, *Sargent* 470 (US). Rio Piedras, *Johnson & Stevenson* 1133 (US). Juana Diaz, *Sintenis* 2894 (L, US). Mayagüez, *Sintenis* 729 (L, S, US). Guayama, Jobas Road, *Goll* 508 (US). Mannabo-Guayama road, *Dale* s.n. (MICH). Bayamon, *Stahl* 850 (L, S). Between Cabo Rojo and San German, *Britton* 4307 (US). Arecibo, *Heller* 342 (US). Ponce, *Goll* 825 (US). Near Ponce on Adjuntas road, *Heller* 6059 (L, US). Aguadilla, *Heller* 4527 (L, US). Yauco, *Underwood & Griggs* 651 (US). VIEQUES ISLAND: Vicinity of Isabel Segunda, *Shafer* 2414 (US). CULEBRA ISLAND: *Britton & Wheeler* 41 (US).

LESSER ANTILLES: U.S. VIRGIN ISLANDS: ST. CROIX: Christiansted, *Rose et al.* 3566 (US). Bassin, *Ricksecker* 84 (L, US). ST. THOMAS: *Friedrichsthal* 29 (W); *Kuntze* ? 546 (US); *Eggers* s.n. (S), 98 (US), 97 (MICH), 261 (L, US); *Oersted* 30 (MICH, S, US). ST. JOHN: *Morrow* 160 (US). BRITISH VIRGIN ISLANDS: TORTOLA: *Fishlock* 15 (US). ST. BARTHÉLEMY: *Forsström* s.n. (S). ANTIGUA: *Box* 1249 dupl. (US). *Rose et al.* 3490 (US). MONTSERRAT: *Shafer* 646 (US). GUADELOUPE: *Forsström* s.n. (S). *Duss* 2670 (US). Moule, *Questel* 807 (US), 808 (US). Morne Miquel, *Questel* 448 (US). Ste. Marguerite, *Questel* 4280 ? (US). MARTINIQUE: *Sieber* 395 (L, PR, W). *Duss* 1361 (US). Fort de France, *H. & M. Stehle* 5734 (US).

TOBAGO: Scarborough, *Broadway* 2956 (L).

VENEZUELA: MIRANDA: Santa Lucía along Río Guaine, *Killip & Tamayo* 37015 (US).

COLOMBIA: MAGDALENA: Santa Marta, *H. H. Smith* 465 (L, S, US). ATLÁNTICO: Barranquilla and vicinity, *Bro. Elias* 332 (US); *Dugand* 5430 (US). Los Pendales at border of Dept. of Bolívar, *Dugand & Jaramillo* 4107 (US). Between Palmar de Varela and Ponedera on the banks of the Magdalena River, *Dugand* 4702 (US). Usiacuri, *Dugand & Barriga* 2367 (US). BOLÍVAR: Cartagena and vicinity, *Billberg* 35 (S), 202 (S); *Dahlin* s.n. (S); *Bro. Heriberto* 330 (US), 273 (US). Ternera, near Cartagena, *Bro. Angel* 772 (US). Vicinity of Turbaco, *Bro. Heriberto* 427 (US). Buenavista, E. of Since, *Pennell* 3986 (US).

BRAZIL: CEARÁ: *Allemão & de Cysneiros* 132 (R, US). Maranguape, *Drouet* 2259 (MICH, US). Serra de Maranguape, *Ule* 9067 (L). Maracanaú, *Ducke* 2607 (US). RIO DE JANEIRO: Cabo Frio, Restinga, *Glaziou* 10327 (P).

This species is characterized by its dense subsessile clusters of flowers in the axils of numerous (15–20) leaves, and by its subglabrous leaves.

26. Melochia nudiflora Standl. & L. Wms. Ceiba 3:122. 1952.

A slender, branched, erect or subscandent shrub 0.9–4.0 meters high, the young stems and petioles tomentose, hairs yellowish brown, stellate, mostly 0.1–0.2 mm. long, forked and simple, 0.5–1.2 mm. long, internodes 1.7–9.0 cm. long; stipules soon deciduous, probably broad judging from the scar; petiole 0.2–3.0 cm. long.

Lamina 3–11 cm. long, 1.0–6.7 cm. wide, ovate to lanceolate, the base rounded to cordate, the apex acuminate to acute, the upper surface subsericeous, covered with appressed simple, and a few forked and stellate, nonoverlapping hairs 0.2–1.3 mm. long, the lower surface subcanescent, tomentulose-sericeous, hairs stellate, simple, and forked, 0.1–1.0 mm. long, both surfaces velvety to the touch, the margin irregularly crenate-serrate, serrations 0.8–3.2 mm. wide, 0.5–2.6 mm. high, 9–14 pairs of primary veins, 2 are basal.

Inflorescences axillary and terminal in subcapitate clusters of 2–15 flowers, the terminal inflorescence extending 1–14.5 cm. beyond the first leaf, with flowers at 1–6 nodes, the axillary inflorescences in the axils of 3–9 leaves, sessile, 1 cm. long, or on branches to about 8 cm. long, the pedicel 0–2 mm. long; bracts 2–6 mm. long, 0.6–3.9 mm. wide, the majority rather broad, suborbicular, ovate to lanceolate, the apex acute to rounded, several at the base of each flower, apparently 2 or 3 sometimes united nearly to the apex, hirsute and ciliate, hairs forked, simple, and stellate, 0.1–1.3 mm. long.

Calyx 4.5–6.4 mm. long, 3.5–5.0 mm. wide, not accrescent, tomentulose-sericeous on the external surface, hairs simple, forked, and stellate, 0.1–1.3 mm. long, tomentulose and canescent at the apex of the internal surface, the teeth 2.4–4.6 mm. long, 1.3–1.9 mm. wide, deltoid- to ovate-acuminate, the sinus acute to narrowly rounded; petals pink, 5.5–7.0 mm. long, 1.5–3.5 mm. wide, obovate–cuneate, attached to the staminal tube for 1–2 mm., the claw 0.7–2.0 mm. long.

Longistylous form. Stamens 3.5–4.0 mm. long, the filaments united up to the anthers, the anther 1.1–1.2 mm. long, 0.7–0.8 mm. wide, oblong, emarginate at both ends, nearly to the middle from the apex; pistil 5.1–5.7 mm. long, the styles 3.2–4.0 mm. long, free to the ovary, papillose at the apex for 0.7–1.0 mm., the ovary densely sericeous, hairs mostly simple, a few forked, 0.7–1.5 mm. long.

Brevistylous form. Stamens 5–5.5 mm. long, the filaments free for 1.7–3.0 mm., the anther 1.1–1.4 mm. long, 0.6–0.9 mm. wide, shape same as that above; pistil 3.0–3.5 mm. long, the styles 1.5–2.2 mm. long, free to the ovary, the ovary globular-ovoid, densely sericeous, hairs simple, 0.5–1.0 mm. long.

Fruit 3.2–4.4 mm. long, 4.5–5.1 mm. wide, obtusely pentagonal, oblate-spheroid, the sulci between the carpels extending a fourth to a third of way to the center of the fruit, hirsute- to sericeous-tomentose, hairs stellate (short), forked, and simple, 0.1–1.0 mm. long, stipe none; dehiscence septicidal into cocci open along the ventral suture; seeds 2.3–2.6 mm. long, 1.6–2.0 mm. wide, trigonal, brown, 1 per cell.

Flowering specimens collected in September, October, December, January, and February; fruiting ones, in October, December, and February.

TYPE LOCALITY: The type, cited below, was collected by Williams and Molina, no. 11234, at Quebrada de Suyapa, Morazán, Honduras, at 1,200 meters elevation.

DISTRIBUTION: Mexico to Costa Rica, in thickets on rocky soil, on limestone hills, in dry forest, or in fields, at 750–1,700 meters elevation.

MEXICO: MORELOS: Cuernavaca, *Pringle* 7342 (MICH). MICHOACÁN: ARTEAGA: Fresnal, *Hinton* 15232 (US). GUERRERO: Near Iguala, *Pringle* 13509 (L, MICH, S). Mountains above Iguala, *Pringle* 8404 (US, W). Iguala Canyon, *Pringle* 10335 (R, S, W). Los Ametes Station, *Pringle* 13818 (MICH, US). CHIAPAS: Tuxtla Gutierrez, *Purpus* 9226 (GH, UC, US). Tuxtla, Hac. Petapa, *C. & E. Seler* 1953 (US).

GUATEMALA: Jacaltenanjo, *Nelson* 3587 (US). GUATEMALA: Near Amatitlán, *Standley* 61394 (MICH).

HONDURAS: MORAZÁN: Barranco de Suyapa, *L. O. Williams & Molina R.* 11234 (US, type and isotype).

COSTA RICA: Rodeo de Pacaca toward the River Yarris, *Pittier* 3228b (US).

This species is close to *Melochia nodiflora* Sw., but it has considerably hairier leaves and stems, generally broader bracts, and inflorescences on naked axillary branches much more commonly than *M. nodiflora*. The petals are usually larger than those of *M. nodiflora*.

27. Melochia tragiifolia Standl. Contr. U.S. Nat. Herb. 23:804. 1923.

A sparsely branched woody plant at least 0.5 meter high, the young stems densely covered with glandular hairs 0.2–0.5 mm. long, a few hairs simple and stellate, 0.2 mm. long, internodes 1.2–6.0 cm. long; stipules deciduous, 2.5–4.5 mm. long, 1.5–3.5 mm. wide, ovate, ciliate, hairs simple to 1.2 mm. long, and simple, forked, stellate, and glandular hairs 0.2–0.3 mm. long on the abaxial surface; petiole slender, 1–2 cm. long, pubescence similar to that of the young stems.

Lamina 3.3–5.2 cm. long, 2.0–3.2 cm. wide, ovate, the base cordate, the apex acute, the upper and lower surfaces green, covered with suberect mostly simple, and a few forked, stellate, and glandular hairs mostly 0.2 (0.1–0.5) mm. long, not overlapping, also ciliate, velvety to the touch, the margin irregularly crenate-serrate to dentate, the teeth 1.8–5.0 mm. wide, 0.5–2.5 mm. high, 7–9 pairs of primary veins, 2 are basal.

Inflorescences on slender axillary branches which are up to 7 cm. long, the flowers in the axils of 1–3 leaves or at up to 3 naked nodes, 3 or 4 flowers in subcapitate umbels at each node, the pedicels 0–3 mm. long; bracts similar to the stipules in size, shape, and pubescence, but sometimes only 1.0 mm. wide.

Calyx 5–6 mm. long, 3.2–4.2 mm. wide, not accrescent, hirsute-tomentose, hairs simple, forked, stellate, and glandular, 0.2–0.7 mm. long, the teeth 2.9–3.2 mm. long, 1.7 mm. wide, ovate, acute to sub-

acuminate, the sinus acute; petals reddish (dried), 8.0–8.2 mm. long, 2.4–3.2 mm. wide, obovate to oblanceolate, the claw 1 mm. long.

Longistylous form. Stamens 4.2 mm. long, the filaments united up to the anthers, the anther 1.3–1.4 mm. long, 0.6–0.9 mm. wide, oblong, emarginate at both ends; pistil sometimes consisting of 6 carpels, 6.1 mm. long, the styles 4.1 mm. long, filiform, clavate and papillose at the apex for 0.7 mm., free to the ovary, hirsute at the base, hairs 0.2 mm. long, the ovary broadly ellipsoid, pentagonal, hirsute, hairs forked and stellate, 0.2–0.6 mm. long.

Brevistylous form not seen.

Fruit 4.5 mm. long, 5.3 mm. wide, globose, obtusely pentagonal, the sulci extending a third of way to the center of the fruit, the midrib subcarinate above the middle of each carpel, covered with simple, forked, and glandular hairs 0.2–0.7 mm. long, the stipe 0.2 mm. long; dehiscence septicidal into cocci open along the ventral suture; seeds not quite ripe, 2.7–3.0 mm. long, 1.7–1.9 mm. wide, red brown, 1 per cell.

Flowering and fruiting specimen collected in March.

TYPE LOCALITY: La Salada, Michoacán, Mexico. The type was collected by Nelson, no. 6927, and is cited below.

DISTRIBUTION: The species is known only from the type locality.

MEXICO: MICHOACÁN: La Salada, *Nelson* 6927 (US, type).

This species is similar to *M. nodiflora* Sw. and *M. nudiflora* Standl. & L. Wms., but it differs in having an abundance of glandular hairs on the calyx and young stems and some on the leaves; the hairs of the latter two are not glandular. The petals are larger than those of *M. nodiflora* and the leaves are not as hairy as those of *M. nudiflora*.

28. Melochia tomentella (Presl) Hemsl. Biol. Centr. Amer. Bot. 1:132. 1879.
PLATE 4

Riedleia tomentella Presl, Rel. Haenk. 2:148. 1835.

A simple or branched, erect, perennial herb to shrub 0.6–2.0 meters high, the young stems and petioles densely tomentulose, hairs stellate, forked, simple, and sometimes also glandular, 0.1–0.3 mm. long, internodes 1.1–3.5 cm. long; stipules soon deciduous, 3.0–5.5 mm. long, 1.0–1.7 mm. wide, lanceolate, hirsute and ciliate, hairs simple, forked, and stellate, 0.1–0.5 mm. long; petiole 0.3–1.8 cm. long, very slender.

Lamina 3.0–9.0 cm. long, 1.2–3.9 cm. wide, lanceolate to ovate, the base rounded, the apex acute to long-acuminate, the upper surface covered with slightly overlapping simple and forked appressed hairs 0.1–0.8 mm. long, the lower surface covered, especially on the veins, with slightly overlapping stellate, forked, and simple hairs 0.1–0.6

mm. long, the margin irregularly crenate-serrate to crenate-dentate, serrations 1.5–6.8 mm. wide, 0.5–2.6 mm. high, 5–10 pairs of primary viens, 2 are basal.

Inflorescences in the axils of 4–12 upper leaves, the clusters sessile or subsessile, subcapitate, 0.7–2.3 cm. long, the peduncle 0–1 cm. long, the pedicel 0–2 mm. long, 2–5 flowers per umbel or head, sometimes also a terminal inflorescence extending 3.5 cm. beyond the first leaf; bracts numerous, 0.5–3.7 mm. long, 0.2–1.0 mm. wide, deltoid-acute to nearly linear, hirsute and ciliate, hairs mostly simple and forked, some stellate and fewer glandular, 0.1–0.7 mm. long.

Calyx 3.1–5.0 mm. long, 3.1–4.0 mm. wide, not accrescent, tomentulose, hairs stellate, forked, simple, and glandular, 0.2 (0.1–0.6) mm. long, the teeth 1.3–3.4 mm. long, 1.2–1.6 mm. wide, deltoid-acute to deltoid-acuminate, the sinus acute to slightly rounded; petals pink or white with pink veins, 5.5–7.8 mm. long, 2.1–3.0 mm. wide, obovate-cuneate, attached to the staminal tube for 1.7 mm., the claw 1.0–1.5 mm. long.

Longistylous form. Stamens 3.8 mm. long, the filaments united up to the anthers, the anther 1.3 mm. long, 0.7–0.8 mm. wide, oblong, emarginate at both ends, nearly to the middle from the apex; pistil 5.3–6.1 mm. long, the styles filiform, slightly clavate at the apex, papillose for 0.8 mm., 4.0–4.5 mm. long, free to the ovary, the ovary ovoid, densely sericeous, hairs 0.3–0.7 mm. long.

Brevistylous form. Stamens 4.8–5.0 mm. long, the filaments free for 2.0 mm., the anther 1.2–1.3 mm. long, 0.9 mm. wide, shape same as that above; pistil 3.6–3.8 mm. long, the styles filiform, papillose for 0.5 mm., 1.7–2.0 mm. long, free to the ovary, the ovary ovoid, densely sericeous-tomentose, hairs up to 0.8 mm. long.

Fruit 3.0–3.8 mm. long, 4.6 mm. wide, depressed-globose, obtusely pentagonal, the sulci between the carpels shallow, extending a third of way to the center of the fruit, densely tomentulose, hairs stellate, forked and simple, 0.1–0.7 mm. long, stipe none; dehiscence septicidal into cocci open along the ventral suture; seeds 2.2–2.6 mm. long, 1.3–1.5 mm. wide.

Flowering and fruiting specimens collected from September to December, and in February.

TYPE LOCALITY: The isotypes, cited below, were collected by Haenke at Acapulco, Mexico.

DISTRIBUTION: Mexico, in shady, short-tree forest bottoms, associated with mesquite, palms, and oaks, at 10–600 meters elevation.

MEXICO: SONORA: ALAMOS: Arroyo Cuchuhaqui, *Gentry* 862 M (MICH). Quiricoba, *Gentry* 833 M (MICH). SINALOA: Vicinity of Culiacan, *Brandegee* s.n. (US). Falda del C. del Jacalito, San Ignacio, *Montes & Salazar* 565 (US). El Norote, *Ortega* 5884 (US). Imala, *Gentry* 4968 (MICH). Rio Fuerte, *Gentry* 943M (MICH). SINALOA?: Ymala, *E. Palmer* 1669 in 1891 (MICH, S, US).

DURANGO: La Bajada, Tamazula, *Ortega* 4322 (US). GUERRERO: Acapulco, *Haenke* s.n. (PR 174404 a–e, isotypes, also US neg. 5548); *E. Palmer* 261 in part 1894–95 (MICH, US). GALEANA: Atoyac, *Hinton* 10908 (MICH, US). Bagueta, *Langlassé* 495 (US). Sierra Madre del Sur, N. of Rio Balsac, Adama, Temisco, Barranca del Consuelo, *Mexia* 8782 (S). OAXACA: JAMILTEPEC: From Collantes to Para Verde, *Conzatti* 4427 (US). From Jamiltepec to Rio Verde, *Nelson* 2375 a (US). Huatulco, *Liebmann* 588–0 (L, US), 11881 fragment (US).

This species is close to *Melochia nodiflora* Sw., but the leaves are usually lanceolate rather than ovate, and acuminate rather than acute, and the stems and leaves are hairier.

Section III. *Melochia*

Section *Riedleia* Griseb. Fl. Brit. W. Ind. 94. 1859.

Perennial or annual herbs to shrubs, 0.2–2 meters high, the taproot not thicker than the base of the stem or 2–3 times thicker, and 0.8–2.0 cm. wide, the young stems subglabrous to cinereous, hirsute, pilose, sericeous or tomentose, hairs stellate, sometimes also forked, simple or glandular, 0.1–3.2 mm. long; internodes 0.3–10.0 cm. long; stipules 1.5–10.0 mm. long, 0.2–3.2 mm. wide, usually lanceolate, deltoid-acuminate or linear, often ciliate, subglabrous to tomentulose, hairs simple, sometimes stellate, forked, and glandular, 0.1–2.7 mm. long; petiole 0.07–6.2 cm. long.

Lamina 0.7–10.5 cm. long, 0.2–8.5 cm. wide, ovate, lanceolate, linear, oblong-ovate, or suborbicular, the base usually rounded, sometimes subcordate, truncate or cuneate, the apex usually acute, sometimes acuminate or rounded, both surfaces glabrous to canescent, hairs simple, appressed, or stellate, forked, and glandular, 0.1–1.0 (–2.2) mm. long, the margin irregularly crenate-serrate, serrations 0.3–12 mm. wide, 0.2–2.5 mm. high, 4–13 pairs of primary veins, usually 2 are basal.

Inflorescences terminal, extending 1–34 cm. beyond the first leaf and axillary, 0.7–19 cm. long, or only terminal or axillary, subcapitate, spicate or paniculate, rarely corymbiform, the peduncle short, 0–1.9 (–4.1) cm. long, the pedicels usually short, 0–9 (–14) mm. long; bracts often long, 0.5–12.2 mm. long, 0.1–1.9 mm. wide, frequently 3 immediately subtending each flower, sometimes 2 united at the base, similar in shape and pubescence to the stipules.

Calyx usually short, 1.4–6.0 mm. long, 2.0–5.0 mm. wide, sometimes membranous, hirsute, sericeous or tomentulose, hairs simple, forked, stellate, or glandular, 0.1–2.3 mm. long, the teeth short, 0.4–2.7 mm. long, 0.2–2.2 mm. wide, the sinus usually rounded to nearly truncate, rarely acute, the teeth often distant; petals white to pink, blue, lilac, violet, purple distally and yellow proximally, red, red striped, yellow or orange, 2.7–12.7 mm. long, 0.8–5.2 mm. wide, usually obovate or

oblanceolate, cuneate, free of the staminal tube or attached to it for 0.3–2.0 (–3.0) mm., the claw 0.2–1.5 (–4.0) mm. long; anther 0.4–1.7 mm. long, 0.3–0.9 mm. wide, oblong, emarginate at both ends, nearly to the middle from the apex, staminodes rarely present, 0.2–0.4 mm. long.

Longistylous form. Stamens 2.6–6.2 mm. long, the filaments united up to the anthers; pistil 3.6–9.0 mm. long, the styles free for 1.5–6.0 mm., to the ovary, or united for 0.5–3.0 mm., papillose for 0.7–2.5 mm. at the apex.

Brevistylous form. Stamens 4.7–8.0 mm. long, the filaments free for 1.7–4.3 mm.; pistil 2.3–6.2 mm. long, the styles free for 1.0–3.8 mm., to the ovary, or united for 0.3–1.8 mm., papillose for 0.7–0.8 mm. at the apex; the flowers of several species not dimorphic, stamens and pistils 1.7–3.2 mm. long, the filaments free for 0–1.2 mm., the styles free for 0.6–1.2 mm., to the ovary, or united for 0.1–0.3 (–0.7) mm.

Fruit 2.4–5.0 mm. long, 3.2–5.5 mm. wide, globular, pentagonal, the sulci between the carpels shallow, extending a fifth to a fourth of way to center of the fruit, often hirsute-tomentulose, hairs simple, sometimes also forked, stellate, or glandular, 0.1–1.5 mm. long, stipe usually none, rarely 0.2–1.0 mm. long; dehiscence all along the dorsal and ventral sutures, tardily septicidal, the fruit falling apart; seeds 1.4–3.2 mm. long, 1.0–1.9 mm. wide, trigonal, brown to black, usually 1 per cell.

The flowering and fruiting periods are usually long, sometimes throughout the year.

TYPE SPECIES: *Melochia corchorifolia* L.

DISTRIBUTION: United States to Argentina, West Indies, Africa, Asia, Pacific Islands, adventive elsewhere in savannas, thickets, or fields, in wet or dry habitats, at 0–2,300 meters elevation.

29. Melochia villosa (Mill.) Fawc. & Rendle, Fl. Jamaica 5:165. 1926. PLATE 5

Usually a perennial, sometimes annual, erect, spreading, decumbent or procumbent, usually branched herb, sometimes suffrutex, rarely a small frutex, sometimes with two to several slender shoots from near the base, 0.3–2.0 meters high, the root as thick as the base of the stem, sometimes 2–3 times thicker and 0.8–2.0 cm. wide, the young stems with a large pith, sometimes hollow, hirsute, villous, lanate, sericeous or tomentose, hairs sometimes ferruginous, tan or golden, simple, forked, glandular, sometimes stellate in longitudinal lines, sometimes predominantly stellate all around the stem, 0.1–2.0 (–2.5) mm. long, internodes (0.3–) 0.6–6.5 cm. long; stipules (2–) 4.2–9.5 mm. long, (0.3–) 0.6–1.7 (–3.1) mm. wide, deltoid- or ovate-acuminate or lanceolate, rarely sublinear or oblong, hirsute-tomentose or seri-

ceous, ciliate, hairs simple, sometimes also forked, stellate, and glandular, 0.1–2.0 mm. long; petiole 0.1–6.2 cm. long, pubescence similar to that of the young stems.

Lamina 1.5–10.5 cm. long, 0.9–8.5 cm. wide, the basal laminae sometimes smaller, usually ovate, sometimes oblong-ovate, lanceolate or suborbicular, the base usually rounded to subcordate, sometimes cordate or truncate, the apex usually acute, sometimes rounded, the upper surface green and subglabrous to hirsute, villous, sericeous, or tomentose and tan-canescent, hairs simple, sometimes also a few forked and stellate, or entirely stellate, rarely as many as 10–12 rays per hair, 0.2–2.0 mm. long, the lower surface green and subglabrous or tan- or ferruginous-canescent, and sericeous or tomentose, hairs simple, glandular, sometimes also forked and stellate or entirely stellate, 0.1–2.0 mm. long, sometimes both surfaces velvety or woolly to the touch, the margin irregularly crenate-serrate, serrations 0.6–4.1 mm. wide, 0.2–2.0 mm. high, (4–) 5–12 pairs of primary veins, usually 2 (–3) are basal, the second pair stronger, veins prominent beneath.

Inflorescences predominantly terminal, usually spicate, sometimes subcapitate, usually coarctate, sometimes lax, extending 1.0–33.5 cm. beyond the first leaf, the flowers at 2–28 nodes, usually 1–5 (–15) flowers at a node, the internodes 0.1–3.0 cm. long, also axillary, 0.7–1.0 cm. long, at 1–6 nodes, rarely flowers at nodes not subtended by leaves on the middle portion of the stem or the terminal inflorescence interrupted by leaves at about 3 nodes, peduncle usually none, sometimes 0.1 cm. long, pedicels none or very short, 0–1.6 mm. long; bracts usually long, 3.5–11.0 mm. long, 0.3–1.0 (–2.5) mm. wide, deltoid-acute to deltoid-acuminate, ovate-lanceolate or lanceolate to sublinear, sometimes subfalcate, 2 or 3 subtending the abaxial side of each flower, merely touching or united at their very base, usually one more below, ciliate and hirsute, sericeous or tomentose, hairs simple and sometimes glandular, forked, or stellate, 0.2–2.0 mm. long.

Calyx 3–6 mm. long, 3–5 mm. wide, hirsute, sericeous or tomentose, sometimes ciliate, hairs simple, sometimes also forked, stellate, or glandular, 0.1–2.0 mm. long, the teeth 0.8–2.5 mm. long, 0.4–2.1 mm. wide, deltoid- to ovate-acute or ovate-acuminate, the sinus acute to rounded and the teeth then rather distant; petals usually pink or purple, sometimes violet, blue, rarely yellow, white, white distally and yellow proximally, or white with pink stripes, 6.0–12.7 mm. long, 1.9–4.5 mm. wide, usually obovate-cuneate, sometimes oblanceolate-cuneate, attached to the stamens for 1.5–3.0 mm., the claw 1–3 mm. long.

Longistylous form. Stamens 3.5–6.2 mm. long, the filaments united up to the anthers, scattered simple, sometimes also forked, hairs 0.1–0.3 mm. long on the tube, the anther 1.1–1.7 mm. long, 0.5–0.9 mm. wide, oblong, emarginate at both ends, nearly to the middle from the apex, sacs slightly spreading at the apex; pistil 5.7–9.0 mm. long, the styles free for 3–5 mm., united for 0.7–1.7 (–2.7) mm., papillose at the apex for 1.8–2.5 mm., the ovary ellipsoid, ovoid or globular, the ovary, particularly the apex, and base of styles rather densely sericeous-tomentose, hairs simple, sometimes also forked and stellate, 0.4–1.5 mm. long, stipe none.

Brevistylous form. Stamens 6–8 mm. long, the filaments free for 2.0–3.4 mm., glabrous or with scattered hairs 0.1–0.2 mm. long, the anther 1.0–1.7 mm. long, 0.5–0.9 mm. wide, shape similar to that above; pistil sometimes consisting of 6 carpels, 3.8–5.2 mm. long, the styles free for 1.5–2.2 mm., united for 0.8–1.5 mm., papillose for 0.8 mm., the ovary ovoid or globular, densely sericeous, hairs 0.5–1.5 mm. long.

Fruit 3.0–3.3 mm. long, sometimes a rostrum 1 mm. long present, 3.4–3.9 mm. wide, globular, slightly depressed, obtusely pentagonal, the sulci between the carpels very shallow, extending a fifth to a fourth of way to the center of the fruit, hirsute-tomentulose, mostly near the apex, hairs simple, sometimes also forked and stellate, 0.1–1.5 mm. long, stipe none; dehiscence loculicidal, first all along the dorsal, then along the ventral suture, tardily septicidal, the fruit falling apart; seeds trigonal, 1.7–2.2 mm. long, 1.1–1.7 mm. wide, reddish brown, usually 1 per cell.

Flowering and fruiting specimens collected throughout the year. According to Gray (20) anthesis is matutinal.

Key to Varieties of *M. villosa*

1. Leaves and stems tomentose or villous-tomentose, tan- or ferruginous-canescent, hairs predominantly or exclusively stellate.
   29c. M. villosa var. **tomentosa**
1. Leaves and stems hirsute-sericeous to subglabrous, hairs predominantly or exclusively simple.
   2. Internodes of terminal inflorescence usually short; bracts typically 1.5 mm. wide; stems not pubescent in 2 longitudinal lines.
      29a. M. villosa var. **villosa**
   2. Internodes of terminal inflorescence long; bracts often up to 2.5 mm. wide; stem pubescent in 2 longitudinal lines (Minas Gerais, Brazil).
      29b. M. villosa var. **regnellii.**

29a. Melochia villosa (Mill.) Fawc. & Rendle var. **villosa**

Sida villosa Mill. Gard. Dict. ed. 8. 1768.
Melochia hirsuta Cav. Diss. 6:323, pl. 175, fig. 1. 1788.
Riedlea serrata Vent. Choix. 37, pl. 37, 1803.
Mougeotia hirsuta (Cav.) H.B.K. Nov. Gen. & Sp. 5:331. 1823.

Riedleia hirsuta (Cav.) DC. Prodr. 1:492. 1824.
Melochia lilacina St.-Hil. Fl. Bras. Merid. 1:162. 1825.
Visenia hirsuta (Cav.) Spreng. Syst. 3:30. 1826.
Visenia serrata (Vent.) Spreng. Syst. 3:30. 1826.
Riedleia serrata Vent. *β glabrescens* Presl, Rel. Haenk. 2:147. 1835.
Riedleia elongata Presl, Rel. Haenk. 2:148. 1835.
Melochia vestita Benth. *in* Hook. Journ. Bot. 4:130. 1841.
Melochia serrata (Vent.) St.-Hil. & Naud. Ann. Sci. Nat. II, 18:36. 1842.
Melochia Clinopodium St.-Hil. & Naud. Ann. Sci. Nat. II, 18:36. 1842.
Melochia densiflora Miq. Linnaea 22:800. 1849.
Riedleja Cubensis Turcz. Bull. Soc. Nat. Mosc. 31(1):209. 1858.
Riedleja Jurgensenii Turcz. Bull. Soc. Nat. Mosc. 31(1):211. 1858.
Riedleja heterotricha Turcz. Bull. Soc. Nat. Mosc. 31(1):211. 1858.
Riedleja tenella Turcz. Bull. Soc. Nat. Mosc. 31(1):212. 1858.
?*Riedleja scutellarioides* Turcz. Bull. Soc. Nat. Mosc. 31(1):210. 1858.
Melochia jurgensenii (Turcz.) Hemsl. Biol. Centr. Amer. Bot. 1:131. 1879.
?*Melochia scutellarioides* (Turcz.) Hemsl. Biol. Centr. Amer. Bot. 1:131. 1879.
Melochia tenella (Turcz.) Hemsl. Biol. Centr. Amer. Bot. 1:131. 1879.
Melochia cephalodes Schum. *in* Mart. Fl. Bras. 12(3):45. 1886.
Melochia hirsuta Cav. var. *grandiflora* Schum. *in* Mart. Fl. Bras. 12(3):46. 1886.
Melochia hirsuta Cav. var. *rotundifolia* Schum. *in* Mart. Fl. Bras. 12(3):46. 1886.
Melochia hirsuta Cav. var. *glabrata* Schum. *in* Mart. Fl. Bras. 12(3):47. 1886.
Melochia hirsuta Cav. var. *glabrescens* (Presl) Gray Syn. Fl. N. Am. 1(1):340. 1897.
Melochia hirsuta Cav. var. *paraguayensis* Chod. Bull. Herb. Boiss. II, 1:403. 1901 (as var. *paraguagensis*).
Riedlea glabrescens (Presl) Small. Fl. SE. U.S. 780. 1903.

The leaves of the typical variety are hirsute-sericeous to subglabrous and not canescent.

TYPE LOCALITY: Jamaica. Miller's type is in the herbarium of the British Museum.

DISTRIBUTION: Southern Florida, Jalisco and Veracruz, Mexico to Paraguay and São Paulo, Brazil, the Greater Antilles, primarily in savanna and pineland, but also in various other habitats, in wet or dry clay, sandy, loam, or serpentine soil, at 0–2,300 meters elevation.

UNITED STATES: "California ad Monte-Rey" *Haenke* s.n. (PR 24355, type of *Riedleia elongata* Presl, also US neg. 5549). The locality is probably incorrect; it is probably somewhere in Mexico. FLORIDA: Near Trabue?, *Simpson* 393 (US). South Florida, *A. W. Chapman* s.n. ?754 (US). LEE: Fort Myers and vicinity, *Hitchcock* 26 (US); *P. C. Standley* 12615 (US), 12961 (US), 18964 (US); *J. P. Standley* 235 (US), 300 (US); *Buswell* 1358a (S). Near Okaloacoochee Slough, Big Cypress, *Small* 8292 (US). Alva, *Francis* 96 (US). Caloosa River, *Garber* 47 (S, US); *Curtiss* 370 A (US), A (S, US). Caloosahatchee, *D. Chapman* s.n. (US). HENDRY: La Belle, *Brass* 15468 (US). HIGHLANDS: Bootheel Creek, Venus, *Brass* 20562 (US).

MEXICO: *Haenke* (W). La Laja, *Liebmann* 588 K (US), 11875 (US), 11877 (US). Sierra San Pedro Nolasco, Talea, etc., *Jurgensen* 506 (K, isotype of ***Riedleja tenella*** Turcz., also US neg. 5414). Passo-Majo, *Wawra* 816 (W).

NAYARIT: About 21 mi. SE. of Tepic, *Gentry* 18343 (US). JALISCO: Guadalajara, Tequila, *E. Palmer* 287 in 1886 (US). Lowlands near Guadalajara, *Pringle* 4452 (MICH, S, US, W). VERACRUZ: Mirador, *Sartorius* s.n. (W). Zacuapan, *Purpus* 12071 (US), 2028 (US), 10877 (US). Xalapa, *Coulter* 793 (GH). Cuitlahuac, *Matuda* 1443 (MICH). SAN ANDRÉS TUXTLA: Between Los Mangos and San Juan de Azúcar, *Dressler & Jones* 205 (US). MEXICO: TEMASCALTEPEC: Cerro Muñeca, *Hinton* 1372 (US). Ixtapan, *Hinton* 1643 (S, US). MICHOACÁN: Coalcoman, *Hinton* 12206 (US). GUERRERO: GALEANA: Moreno, *Hinton* 14343 (MICH, US). Montes de Oca: Vallecitos, *Hinton* 11371 (US). OAXACA: Near Santo Domingo, *Nelson* 2706 (US). Rincón Antonio, *Orcutt* 3271 (GH, US). From Cordoba to Santa Lucrecia, *Conzatti* 1716 (US). About 2 km. E. of Zantepec, *King* 1877 (US). CHIAPAS: Chicomuselo, *Matuda* 4430 (US). Acapetagua, *Matuda* 16684 (MICH). Near the junction of Rio Perlas and Rio Jataté at San Quintin and near Laguna Miramar, *Sohns* 1647 (US).

GUATEMALA: Los Amates, *Deam* 121 (MICH). PETÉN: Big Fall Pine Ridge, *Lundell* 4185 (S). La Libertad and vicinity, *Lundell* 2301 (MICH), 2389 (MICH), 2612 (MICH); *Aguilar H.* 172 (MICH). Sabana Zotz, *Lundell* 3582 (MICH). HUEHUETENANGO: Cerro Victoria, across the river from Finca San Rafael, Sierra de los Cuchumatanes, *Steyermark* 49569 (US). ALTA VERAPAZ: Cubilgüitz, *Türkheim* 7615 (US), II 49 (S). Cajabon near Finca Sepacuite, *Cook & Griggs* 330 (US). Between Cajabon and Secanquim, *Goll* 108 (US). Chamá, *Johnson* 836 (US). Rútzul, between Cajabon and Lanquin, *Goll* 120 (US), 131 (US), 132 (US). IZABAL: Cristina, *Blake* 7568 (US). SANTA ROSA: Las Viñas, *Heyde & Lux* 6074 (US). Rio de las Cañas, *Heyde & Lux* 3953 (US).

BRITISH HONDURAS: *Record* s.n. (US). Honey Camp, Coastal Region, *Lundell* 585 (US). Maskall Pine Ridge, *Gentle* 1044 (MICH, S). Butcher Burn, Sibun River, *Bartlett* 11413 (MICH, S), 11384 (MICH). All Pines, *Schipp* 549 (MICH, S). Belize River, *Lundell* 4185 (MICH). Near Manatee Lagoon, *Peck* 297 (GH). BELIZE: Baker's Pine Ridge, *Lundell* 3793 (MICH). TOLEDO: Swasey Branch, Monkey River, *Gentle* 3771 (MICH).

HONDURAS: COPÁN: Hac. Espiritu Santo to Quebrada Majanales, *Blake* 7463 (US). COMAYAGUA: Vicinity of Siguatepeque, *Standley* 56272 (US); *Yunker et al.* 5540 (MICH, S).

SALVADOR: MORAZÁN: About 1.6 km. SE. of Divisadero, *Tucker* 580 (US).

NICARAGUA: Slopes of Mt. Mombacho, near Granada, *Grant* 758 (GH).

COSTA RICA: Hac. "La Argentina," Grecia, *Valerio* 600 (US). Buenos Aires, *Tonduz* 4028 (US). Infiernillo cerca de Juan Viñas, *Tonduz* 10416 (US). Boruca, *Pittier* 4583 (US). Rodeo, *Pittier* 1647 (US). Las Cóncavas, near Cartago, *Cooper* 13 (US); *Lankester* 323 (S); *Stork* 2145 (MICH). Paraiso Cartago, *Torres* 101 (US), 191 (US).

PANAMA: CHIRIQUÍ: San Carlos, *Roy* 4 (MICH, US). Sabana de la Tortuga, between El Boquete and Caldera, *Pittier* 3304 (US). Vicinity of Boquete, *W. L. Stern et al.* 1175 (US). COCLÉ: Aguadulce, *Pittier* 4858 (US). CANAL ZONE: Along the old Las Cruces Trail, between Ft. Clayton and Corozal, *Standley* 29087 (US). Chiva-Chiva Trail, Red Tank to Pueblo Nuevo, *Piper*, 5757 (US). PANAMÁ: Sabanas and vicinity, *Bro. Paul* 74 (US); *Standley* 25845 (US), 25934 (US); *Bro. Gervais* 159 (US); *Killip* 3122 (US). Río Tapia, *Standley* 28300 (US). Near Río Tapia, Juan Díaz, *Maxon & Harvey* 6632 (S, US). Between Matías Hernández and Juan Díaz, *Standley* 28897 (S, US), 31980 (US). Matías Hernández, *Pittier* 6797 (US), 6875 (US). Sabana de Juan Corso, near Chepo, *Pittier* 4510 (US). Along the road between Panamá and Chepo, *Dodge et al.* 16660 (S). Nuevo San Francisco, *Standley* 30748 (US). Near the big swamp E. of the Río Tecumen, *Standley* 26506 (US).

CUBA: *Poeppig* s.n. (S). *de la Sagra* s.n. (W). Laguna los Piedras, ?*Poeppig*, collected 1824 (W). S. Cristobal, *C. Wright* 2086 (S, US), 2088 (S, US). Isle of Pines: *Taylor* 94 (US). Near Nueva Gerona, *Curtiss* 218 (L, US); *W. Palmer & Riley* 867 (US); *Killip* 42538 (US). Near Managua, *W. Palmer & Riley* 1079 (US). Las Tunas, *Britton & Wilson* 14745 (US). Santa Ana, *Ekman* 12206 (S). Pinar del Río: Pinar del Río, Pinar del Cajalbana, *Ekman* 10438 (S). Arroyo del Sumidero, *Shafer & Bro. Leon* 13567 (US). Palm barrens W. of Guane, *Shafer* 10418 (US), 10645 (US). N. of San Diego de los Baños, *W. Palmer & Riley* 630 (US). El Guama, *W. Palmer & Riley* 129 (US). S. of Las Mangas, *Ekman*, 13060 (S). Between Candelaria and Artemisa, *Wilson* 1716 (UC). Las Villas: Near Santa Clara, Howard 5600 (US). cienfuegos: Cieneguita, *Combs* 217 (US). Camaguey: Sierra Cubitas to Santa Rosa, *Shafer* 548 (US). Oriente: Sierra Maestra at Pinar de Caridad, SE. of Yara, *Ekman* 14685 (S).

HAITI: Dept. du Nord: Vicinity of Dondon, *Leonard* 8649 (US). Massif du Nord: Le Borgre, Poste Marie Congo, *Ekman* H. 4844 (S, US). Massif de la Hotte, western group, Corail, at Dutreuil, *Ekman* H. 10745 (S).

DOMINICAN REPUBLIC: Loma Mata Clara, *Eggers* 2336 (L, US). La Nassa, *Faris* 135 (US). La Leonor, *J. S. Jiménez* 2407 (US). Santa Domingo: Vicinity of Ciudad Trujillo, *Allard* 14237 (US), 14232 (US). Sabana de Santa Rosa, *Allard* 15892 (US), 15942 (US), 16023 (US). Moca: Villa Altagracia, *Ekman* H. 11230 (S, US). Duarte: 33 km. de la Carretera, *J. Jiménez* 821 (US). Valle de Cibao, Pimentel, *Ekman* H. 13239 (S). La Vega: Sierra Prieta, *J. S. Jiménez* 1148 (US). Trujillo: Vicinity of Piedra Blanca, *Allard* 13503 (US), 13831 (S, US), 18896 (US). Pacificador: Villa Riva (Almacén), *Abbott* 536 (US), 626 (US). Seibo: Vicinity of Higüey, *R. A. & E. S. Howard* 9874 (US). Guarabo, SE. of Jovero, *Abbott* 2762 (R, S, US), 2820 (US).

JAMAICA: *W. Wright* s.n. (W). Oxford, *Harris* 9428 (US). Clarendon: Clarendon Park to Four Paths, *Britton* 3788 (US). James Hill Savanna, *Harris* 12842 (US). Kellits, *Harris* 11151 (US). Hollis' Savanna, *Harris* 12251 (S, US). Hanover: Orange Bay Morass, *Macfadyen* s.n. (S).

PUERTO RICO: *Sintenis* 5922 (US). *Goll* 43 (US). *Stahl* 350 (L). Near Cabo-Rojo at Port Real, *Sintenis* 162 b (L, US, W). Near Santurce, *Heller* 251 (US), 4671 (US); *Coules* 158 (US). Moca, *Sargent* 248 (US). Rio Piedras, *Stevenson* 112 (US). Sabana Abajo, near Carolina, *Britton & Brown* 5712 (US). Bayamón, *Underwood & Griggs* 865 (US). Along the road to Rosario, Las Mesas, *Theoslohn* 219 (GH).

TRINIDAD: Piarco Savannah: *Broadway* 2132 (US); *Warming* 262 (US). S. of Arouca, *Britton et al.* 58 (US). S. of Dabadie, *Britton & Hazen* 695 (US).

FRENCH GUIANA: *Le Prieur* 129? (L). Cayenne and vicinity, *Broadway* 152 (US), 608 (US); *Sagot* 55 (S, W). Maroni, *Melinon* 45 (US).

SURINAM: Bergendaal, *Focke* 359 (L). Epereroe, *Pulle* 495 (L, US).

BRITISH GUIANA: *Schomburgk* 133 (W, syntype of *Melochia vestita* Benth., also F neg. 35388 ex. P). Between Takutu River and Kanuku Mts., *A. C. Smith* 3267 (S, US). Rupununi: 45 mi. N. of Lethem, *Irwin* 835 (US).

VENEZUELA: Sucre: Cumana, Guanaguana, *Funck* 170 (LE, isotype of an unnamed variety of *Riedleja heterotricha* Turcz.). Los Altos, *Tamayo* 2163 (US). Anzoátegui: Bajos del Rio Tigre, in Cristovero, SE. of San Tomé, *Pittier* 14595 (US). Rio Caris near El Tigre, *Pittier* 14321 (US). Aragua: Colonia Tovar, *Fendler* 1935 (GH). Above Guamitas, *Ll. Williams* 10356 (US). Valle de Guamitas, Parque Nacional, *Pittier* 15251 (US). Carabobo: Near San Joaquin, *Pittier* 8007 (US). Trujillo: Near La Ceiba, *Reed* 949 (US). Zulia: Vicinity of Mene Grande, *Pittier* 10575 (GH, US). Apure: Puerto Paez, *Velez* 2724 (US).

BOLÍVAR: Morichal Santa Isabel, *Cardona* 660 (US). Calcetas en la Pica de El Cristo, *Cardona* 1020 (US). Rio Aprada afluente del Uriman, Caroni, Guayana, *Cardona* 2002 (US). GRAN SABANA: Cercanias de Santa Elena, *Tamayo* 3215 (US). ?BOLÍVAR: Camarata Valley, *Simpson* 66 (US). AMAZONAS TERR.: Maypures, *Spruce* s.n. (K).

COLOMBIA: *Linden* 887 collected 1842 (W). MAGDALENA: La Jagua, *Haught* 3648 (US). ?MAGDALENA: Queremal Jagua, *Arbeláez* 3010 (US). NORTE DE SANTANDER: Ocaña, *Schlim* 94 (P). REGION DEL SARARE: El Barco, *Cuatrecasas* 13174 A (US). SANTANDER: SAN GIL: Hacienda de La Mesita, *Langenheim* 3312 (US). CUNDINAMARCA: Paime, *Bro. Ariste-Joseph* A802 (US). Melgar, *Pennell* 2918 (US). Ibama, E. of Yacopi, *Grant* 9143 (US). El Colegio, *Schneider* 928 (S). META INT.: Villavicencio and vicinity, Apiay, *Humbert & Fernandez* 27182 (P), 27193 (P); *Jaramillo el al.* 293 (US). E. Mico Airstrip, E. savanna before Rio Guejar, *Philipson et al.* 1316 (US). Boca de Monte, Llanos de San Martin, *S. G. Smith & Idrobo* 1438 (US). ARAUCA: RIO CASANARE: Esmeralda, *Cuatrecasas* 3959 (US). (This specimen approaches *M. villosa* var. *tomentosa*). VAUPÉS: Caño Cuduyari, *Cuatrecasas* 7225 (US). Rio Vaupés, at Mitu, *Humbert & Fernandez* 27211 (P, US). TOLIMA: Mariquita and vicinity, *Garcia Barriga* 8128 (US); *Pennell* 3659 (US). W. of San Lorenzo, *Pennell* 3459 (US). HUILA: Cordillera Oriental, E. of Neiva, *Rusby & Pennell* 476 (US). N. of Neiva, upper basin of Río Magdalena, *S. G. Smith* 1120 (US). San Augustin, *Bro. Daniel* 4132 (US). One km. SW. of San Antonio Fortalecillas, *Fosberg* 19833 (US). ANTIOQUIA: Medellín, *Archer & Aguilar* 702 (US). VALLE DEL CAUCA: Rio Bolo, *Dryander* 337 (US). Palmira, *Pennell & Killip* 6045 (US). Timba, *von Sneidern* 1268 (S, US), 1185 (S). Samaria, 2 km. W. of Timba, *Fosberg* 20522 (US). CAUCA: El Tambo, *Idrobo & Fernandez* 123 (US). Jamundi, Cauca Valley, *Pittier* 1508 (US). Aganche, *Pennell & Killip* 8318 (US).

ECUADOR: "Yapio cerca Quilichao," *Jameson* s.n. (US). Cañar, *Rose et al.* 23793 (US).

PERU: SAN MARTÍN: San Roque, *Ll. Williams* 7102 (S, US); *Melin* 123 (S). Tarapoto, *Ll. Williams* 6149 (S); *Ule* 6528 (L). Zepelacio, near Moyobamba, *Klug* 3705 (S, US). Rioja, *Woytkowski* 6084 (US).

BOLIVIA: BENI: Lake Rogagua, *Cardenas* 1628 (US). SANTA CRUZ: SARA: Buena Vista, *Steinbach* 6943 (S), 5104 (A).

BRAZIL: Martii Herb. Fl. Bras. 582 (L). *Pohl* s.n. (W). Pirapora, Independencia, *Burret et al.* 10104 (R). Western part, *Tamberlik* s.n. (W). RIO BRANCO: Serra Pellada, *Ule* ?7634 (L). AMAZONAS: São Gabriel, Rio Negro, *Holt & Blake* 625 (RB, US). Rio Içana, Tunuí, *Black* 48–2597 (US). PARÁ: Vicinity of Santarem, *Spruce* June 1850 (W). Almeirim, Rio Arayollos, *Ducke* s.n. (RB). PIAUÍ: *Gardner* 2488 (US, syntype of *Melochia vestita* Benth.). BAHIA: *Glocker* 425 d(S). *Blanchet* 1588 (W). Jacobina, *Blanchet* 3663 (P, US, W, also US neg. 5666 ex P). Serra do S. Antonio, F neg. 9599 ex B of *Sello* 1935, syntype of *Melochia cephalodes* Schum. (US). MINAS GERAIS: Lassance-Pirapora, *Cochran* s.n. (R, US). Corinto, *Mexia* 5530 (S, US). Rio Arassuahy, *Glaziou* 12460 (R). Morro de Caxambú, *Glaziou* 15849 (R). São Sebastião do Paraiso, *Brade & Altamiro* 45 (R). Lagoa Santa, *Hoehne* 6140 (R). S. João d'El Rey, Casa da Pedra, *Armond* s.n. (R). Caldas, *Mosén* ?4023 (S), 4024 (S). ITUIUTABA: S. Terezinha, *Macedo* 1643 (RB), 3177 (US). Certaó, Caeduis, Tapeira, near S. Francisco River, *St.-Hilaire* ?1823 (P, isotype of *Melochia lilacina* St.-Hil., also US neg. 5672). GOIÁS: *Gardner* 3030 (US, W). Planalto, *Glaziou* 20734 (S). Between Conceição and Natividade, *Burchell* 8168 (GH). At Megaponte, Rio Uruhú, *Pohl* 1096 (W). Twenty km. N. of São João da Aliança, region of the Chapada dos Veadeiros, *Dawson* 14247 (US). MATO GROSSO: Cuyabá, *Malme*

2633 (S). Coxipó da Ponte O. (Cuyabá), *Hoehne* 2982 (719) (R). Tapirapoan, *Hoehne* 1280 (R). SÃO PAULO: Near Batataes, *Riedel & Luschnath* 2243 (LE). Itú, *Riedel & Luschnath* 1992 in part (LE, US neg. 5274, det. as *M. hirsuta* Cav. var. *macrophylla* Schum. by Schumann). Moji-Guaçu, *Eiten & Machado de Campos* 1534 (US).

PARAGUAY: In regione cursas superior flumenis Y-acá, Cordillera Central near Piribebuy, *Hassler* 6748 in part (P, S).

This species is related to *Melochia splendens* St.-Hil. & Naud., but the inflorescence of the latter is primarily axillary rather than primarily terminal. It is also close to *Melochia savannarum* Britt., but the latter generally is a smaller, more prostrate plant with smaller leaves and a shorter terminal inflorescence with fewer flowers at a node.

29b. Melochia villosa (Mill.) Fawc. & Rendle var. **regnellii** (Schum.) A. Goldberg, comb. nov.

Melochia hirsuta Cav. var. *Regnellii* Schum. *in* Mart. Fl. Bras. 12(3):46, pl. 10. 1886.

The leaves of this variety have few, scattered, mostly simple hairs; the stipules are broader than those of the other varieties; the stem is pubescent in two longitudinal lines; and the internodes of the terminal inflorescence are long.

TYPE LOCALITY: Caldas, Minas Gerais, Brazil. The lectotype, *Regnell* III 278, is cited below.

DISTRIBUTION: Minas Gerais, Brazil.

BRAZIL: MINAS GERAIS: *Widgren* s.n. (R, S). Caldas, *Regnell* III 278 (S, lectotype of the variety; R, US, isotypes of the variety); *Lindberg* 284 C(S).

29c. Melochia villosa (Mill.) Fawc. & Rendle var. **tomentosa** (Schum.) A. Goldberg, comb. nov.

Melochia hirsuta Cav. var. *macrophylla* Schum. *in* Mart. Fl. Bras. 12(3):47. 1886.

Melochia hirsuta Cav. var. *calophylla* Schum. *in* Mart. Fl. Bras. 12(3):47. 1886.

Melochia hirsuta Cav. var. *tomentosa* Schum. *in* Mart. Fl. Bras. 12(3):47. 1886.

Melochia subcordata Morong, Ann. New York Acad. Sci. 7:62. 1892.

Melochia hirsuta Cav. var. *tomentosa* Schum. f. *ferruginea*, f. *albiflora*, and f. *minus induta*, all Schum. & Hassl. Bull. Herb. Boiss. II, 4:72. 1903.

The leaves and stem of this variety are much hairier than those of the typical variety. They are tomentose or villous-tomentose, and usually tan- or ferruginous-canescent. The hairs are predominantly or exclusively stellate, in the other varieties they are predominantly or exclusively simple.

TYPE LOCALITY: Goiás and São Paulo, Brazil. The lectotype, Riedel no. 1992 dupl. 16, is cited below.

DISTRIBUTION: Venezuela to northern Argentina.

VENEZUELA: APURE: ALTO-APURE: Hato Matapalo, *Jahn* 212 (US).
BRAZIL: *Riedel* 1992 dupl. 16 (W, lectotype). *Regnell* III 277a (S). Villa

Boa, *Pohl* 1232 (W). Western Brazil, *Tamberlik* s.n. (W). ?Rio Branco: *Kuhlmann* 417 (US). Minas Gerais: *Claussen* 96 (GH, P, S). *Pires & Black* 3064 in part (US). Uberaba, *Regnell* III 277 in part (S, US). Bello Horizonte, *Barreto* 7858 (R). Bello Horizonte and Bairro do Bomfim, *Magalhães* 78 (R). ?Morro de Caxambú, *Glaziou* ?15849 (K). Lagoa Santa, *Warming* s.n. (S). Porto Alegre, *Regnell* III 277 in part (S). Before Rib. do Frada, *Pohl* 3281 (W). sêrro: 3 km. from Sêrro, *L. O. Williams & Assis* 6851 (US). Rio das Pedras ao Vallú, *Glaziou* 18901 (R). Goiás: Mossamedes, *Ule* 487 (R, US). Near city of Goiás, *Burchell* 6641 (GH, syntype of *M. hirsuta* Cav. var. *calophylla* Schum.), 6920 (GH). ?Goiás: F neg. 19636 of Pohl? dupl. 517 (US, syntype of *M. hirsuta* Cav. var. *calophylla* Schum.). Mato Grosso: Bomfim, *Diogo* 268 (R, US), 241 (R). Triumpho, Rio S. Laurenço, *Hoehne* 4561 (R). Cuiabá, *Hoehne* 4881 (711) (R); *Malme* 1292 (S). São Paulo: Batataes, *Regnell* III 277 in part (S). Itú, *Riedel & Luschnath* 1992 in part (LE, US neg. 5267).

PARAGUAY: Near Bellavista (Apa), *Hassler* 7758 (S, W). Villarrica, *Jorgensen* 3809 (S, US). Cerro Noaga, *Anisits* 2846 (S). Between Rio Apa and Rio Aquidaban, Centurion, *Fiebrig* 4276 (L). In region of River Alto Paraná, *Fiebrig* 6392 (US). Road to "Yerbales" montum "Sierra de Maracayú," *Hassler* 5584 (W). Cordillera de Altos, *Hassler* 3599 (W). Sierra de Amambay, *Rojas* in *Hassler* 10006 (W). Central Paraguay, *Morong* 292 (US, isotype of *Melochia subcordata* Morong). Caazapa: Borja, *West* 8544 (UC). In regione cursus superior flumenis Y–Acá, Cordillera Central near Piribebuy, *Hassler* 6748 in part (W).

ARGENTINA: Formosa: Colonia Clorinda, *Venturi* 9098 (US). Corrientes: mourucuyá: Est. Santa Teresa, Tacuaral, *Cristóbal et al.* 10 (UC). general paz: Los Cubanos, *Schwarz* 275 (S). paso de los libres: Pueblo Paso de los Libres, *Ibarrola* 2051 (US). berón de astrada: ?Chuicho, *Schwarz* 333 (US). Misiones: Posadas, Loreto, bank of River Alto-Paraná, *Ekman* 187 (S). At River Yabebiry, *Ekman* 1974 (S). candelaria: Loreto-Rinconada de Yabebiry, *Montes* 5?, February 1946 (UC).

30. Melochia savannarum Britt. Mem. Torr. Bot. Cl. 16:81. 1920.

A prostrate or erect herb to suffrutex with several branches from the base and sometimes branched above, 0.2–0.6 meter long, the root woody, thickened, 0.9 cm. wide, the young stems tomentulose, hairs stellate, 0.1–0.3 mm. long, usually also forked and simple hairs 0.5–1.7 mm. long, few glandular hairs 0.3–0.6 mm. long, internodes 0.7–2.7 cm. long; stipules 2.2–3.6 mm. long, 0.5–0.7 mm. wide, lanceolate, ciliate, hairs simple, 0.3–0.8 mm. long; petiole 0.07–0.5 (–0.8) cm. long, pubescence similar to that of the stems but with long hairs more abundant.

Lamina 1.0–2.2 cm. long, 0.7–1.8 cm. wide, ovate, rarely also suboblong, the base rounded to truncate, rarely subcordate, the apex rounded to subacute, hairs on upper surface simple, appressed, 0.3–1.3 mm. long, sometimes also stellate, forked, sometimes also ciliate, hairs glandular and simple, 0.5 mm. long, sometimes glabrate, the lower surface with few to numerous stellate hairs 0.1–0.3 mm. long, and simple somewhat appressed hairs 0.3–1.0 mm. long, the latter type may be absent or predominant, the margin irregularly dentate, serrate or

crenate-serrate, serrations 0.9–4.0 mm. wide, 0.5–2.1 mm. high, extending to the base of the leaf, 4–6 pairs of primary veins, 1 or 2 are basal.

Inflorescences terminal and in the axils of the upper 1–6 leaves, subcapitate, 2–6 flowers in a cluster, less than 1 cm. to 4 cm. long, with flowers at 1–3 nodes, peduncle none, the pedicels 0.5–2.0 mm. long; bracts 2.5–5.8 long, 0.2–1.0 mm. wide, lanceolate to linear, usually 3 immediately subtending the flower, others sometimes present below, rarely 2 united part way, mostly ciliate, hairs simple, 0.3–1.0 mm. long, sometimes also a few glandular and fewer forked and stellate hairs, 0.3 mm. long.

Calyx 3.0–4.8 mm. long, 3.0–4.7 mm. wide, hirsute-tomentose, hairs simple, forked, and stellate, 0.1–1.0 mm. long, the teeth 1.0–1.8 mm. long, 0.8–1.8 mm. wide, deltoid-acute, the sinus rounded to acute; petals blue, pinkish blue, pink and pale toward the base, nearly white with a faint tinge of violet, 5.2–9.0 mm. long, 2.1–4.5 mm. wide, obovate, obovate-oblong, or obovate-cuneate, the claw 0.5–1.0 mm. long, the base free of staminal tube or attached to it for 0.5–1.5 mm.

Longistylous form. Stamens 3.5–4.4 mm. long, the filaments united up to the anthers, occasionally a staminode 0.4 mm. long present, a few simple hairs 0.1–0.2 mm. long on the filament tube, the anther 1.2–1.5 mm. long, 0.6–0.7 mm. wide, oblong, rather deeply emarginate at both ends, nearly to the middle from the apex; pistil 5.2–6.2 mm. long, the styles free for 2.0–4.0 mm., united for 0.5 mm., papillose at the apex for 1.5–2.0 mm., the ovary ellipsoid to ovoid, tomentulose, hairs 1.0 mm. long, stipe none.

Brevistylous form. Stamens 4.7–6.8 mm. long, the filaments free for 2.5–2.7 mm., very few simple hairs 0.1 mm. long on the filaments and filament tube, the anther 1.1–1.4 mm. long, 0.6–0.8 mm. wide, shape similar to that above; pistil 2.3–4.0 mm. long, the styles filiform, recurved, free for 1.0–1.5 mm., united for 0.6 mm., the ovary ovoid, tomentulose, hairs 0.2–1.0 mm. long.

Fruit 3.0–3.2 mm. long, 3.4–3.9 mm. wide, globular, pentagonal, the sulci between the carpels very shallow, extending about one-fifth of way to the center of the fruit, hirsute-tomentulose, hairs simple and forked, 0.1–1.0 mm. long, stipe none; dehiscence loculicidal along the dorsal suture, eventually also septicidal; seeds 1.8 mm. long, 1.2 mm. wide (unripe 2.0–2.5 by 1.1–1.9 mm.), trigonal, dark brown, 1 per cell.

Flowering specimens collected from December to April, and in June and August; fruiting ones, from December to February and in June.

Type locality: Herradura, Pinar del Río, Cuba, in savannas and along streams; type collected by Earle, no. 639, cited below.

Distribution: Isle of Pines and Pinar del Río, Cuba, in white sand,

tall-grass savanna, in sandy pinelands, in wet or dry habitats, near sea level and on uplands.

CUBA: Isle of Pines: Near Playa Nueva Gerona, *Killip* 44515 (US). Cerro de Cunagua, *Killip* 43669 (US). San Francisco de las Piedras, *Killip* 43549 (US). Along the road to Playa, *Killip* 42996 (US). San Pedro region, *Killip* 43697 (US). Columbia, *Killip* 43575 (US). Río Júcaro region, *Killip* 42941 (US). Playa Roja, *Killip* 43185 (US). Pinar del Río: Herradura, *Earle* 639 (NY, type); *Britton et al.* 6518 (US); *Ekman* 10730 (S). El Sábalo, Finca Sabanalamar, *Killip* 32253 (US). Sábalo, *Ekman* 16753 (S). Near Pinar del Río, *W. Palmer & Riley* 448 (US). Laguna Santa Maria, S. of Rio Feo, *Ekman* 17267 (S).

This species is close to *M. villosa* (Mill.) Fawc. & Rendle, but it is generally a smaller, more prostrate plant with fewer flowers at a node, a shorter terminal inflorescence, and smaller leaves. Usually the apex of the lamina is rounded, but usually acute in *M. villosa*.

31. Melochia splendens St.-Hil. & Naud. Ann. Sci. Nat. II, 18:36. 1842.

An erect subsimple suffrutex at least 0.45 meter high, the young stems and petioles densely tomentose, tan-canescent, hairs 0.3–2.3 mm. long, internodes 1–3.1 cm. long; stipules 5.2–10 mm. long, 1–3.2 mm. wide, oblique-ovate or lanceolate, sericeous-tomentose, hairs simple, 1 mm. long, and stellate, 0.1 mm. long; petiole short, 0.1–0.4 cm. long.

Lamina 2.3–5.7 cm. long, 1.1–2.6 cm. wide, lanceolate to ovate, the base cuneate to rounded, the apex acute to somewhat rounded, silky and woolly to the touch, both surfaces tan-canescent, densely tomentose, and sericeous, hairs 0.2–1.5 mm. long, short ones stellate, long ones simple, the margin irregularly crenate-serrate, serrations 0.6–2.8 mm. wide, 0.2–0.8 mm. high, 8 or 9 pairs of primary veins, 2 are basal.

Inflorescences mostly axillary in the axils of 4–15 leaves, sometimes a few of the middle ones not subtended by a leaf, sometimes apparently also terminal, 1–1.4 cm. long, subcapitate, in clusters of 2–5 flowers, penduncle none, the pedicels 0–1 mm. long; bracts 10.8–12.0 mm. long, 1.0–1.3 mm. wide, 4 immediately subtending a flower, 2 united at the very base, lanceolate-acuminate, densely tomentose and sericeous, hairs 0.1–2.0 mm. long.

Calyx 5.0–5.2 mm. long, 2.9–3.2 mm. wide, densely sericeous, hairs 1–2.3 mm. long, some stellate, 0.1 mm. long, the teeth 1.5–2.3 mm. long, 1–1.5 mm. wide, deltoid-acuminate with rounded sides, the sinus acute to somewhat rounded; petals 9.6–10.0 mm. long, 1.7–2.0 mm. wide, oblanceolate, attached to the staminal tube for 2 mm., the claw 2–4 mm. long.

Longistylous form not seen.

Brevistylous form. Stamens 7–8 mm. long, the filaments free for

2 mm., a few hairs 0.1–0.2 mm. long on the filament tube, the anther 1.2–1.4 mm. long, 0.6 mm. wide, oblong, emarginate at both ends; pistil 6–6.2 mm. long, the styles filiform, papillose for 0.7 mm. at the apex, free for 2.7–3.0 mm., united for 1.7–1.8 mm., the ovary ovoid, sericeous, hairs 1–2 mm. long.

Fruit (one present) with 4 carpels aborted, 2.5 mm. long, 2.1 mm. wide, sericeous, hairs 1–1.5 mm. long, stipe none; dehiscence loculicidal all along the dorsal suture; seeds 2 mm. long, 1.1 mm. wide, brown, 1 per cell.

TYPE LOCALITY: Goiás, Brazil. The type was collected by Gardner, no. 3601, and is in Herbier Delessert.

DISTRIBUTION: Goiás, Brazil, also Piauí, Brazil, according to Schumann (47), and Arauca, Colombia.

COLOMBIA: ARAUCA: RÍO CASANARE: Esmeralda, *Cuatrecasas* 3855 (US).
BRAZIL: GOIÁS: F neg. 9607 ex B of *Gardner* 3601, isotype (US); *Burchell* 8587 (GH).

This species is close to *Melochia villosa* (Mill.) Fawc. & Rendle, but differs by having axillary rather than terminal inflorescences and generally narrower leaves, often lanceolate, and cuneate at the base, rather than ovate leaves rounded or cordate at the base.

32. Melochia bracteosa F. Hoffm. Beitr. Fl. Centr.-Ost-Afr. 13. 1889.
Melochia crinita R. Br. MS. *in* Hiern Welw. pl. 1:90. 1896.
Melochia Welwitschii Hiern, Welw. pl. 1:90. 1896.
Melochia melissifolia Benth. var. *microphylla*, var. *brachyphylla*, var. *bracteosa* (F. Hoffm.), var. *Welwitschii* (Hiern), var. *mollis*, all K. Schum. *in* Engl. Mon. Afr. Pfl. 5:42. 1900.
Melochia mollis Hutch. & J. M. Dalz. Kew Bull. 297. 1928.

An herb or undershrub about 1 meter high, the young stems and petioles densely covered with simple hairs, sometimes also stellate, forked, and glandular, 0.2–3.2 mm. long, the internodes 2–6.5 cm. long; stipules 8–10 mm. long, 1–2.8 mm. wide, lanceolate, ciliate and hirsute, hairs simple, sometimes also forked, 0.2–2.7 mm. long; petiole 0.3–2.3 cm. long.

Lamina 3.5–8.5 cm. long, 1.2–4.3 cm. wide, lanceolate to ovate, the base rounded to subcordate, the apex acute, both surfaces sericeous, woolly or velvety to the touch, hairs simple, sometimes also forked stellate, and glandular, 0.2–2.2 mm. long, the margin irregularly crenate-serrate, serrations 0.5–3.6 mm. wide, 0.4–2.0 mm. high, 7–11 pairs of primary veins, 2 or 3 are basal.

Inflorescences 1–4.8 cm. long, in the axils of 10–14 or more leaves, sometimes 2 clusters per axil, 2–10 flowers per cluster, the peduncle 0–3.0 cm. long, the pedicels 0.5–3.5 cm. long; bracts sometimes 2 united at the very base, (3.5–) 5.2–12.2 mm. long, 0.3–1.5 mm. wide,

lanceolate to sublinear, sometimes falcate, ciliate and hirsute, hairs simple, sometimes also glandular, 0.2–3.2 mm. long.

Calyx membranous, 3.0–4.5 mm. long, 2.6–4.3 mm. wide, hirsute-sericeous, hairs simple, 0.2–2.0 mm. long, mostly near the apex, the teeth 1–2 mm. long, 0.8–1.7 mm. wide, deltoid, acute to acuminate, the sinus broadly rounded, teeth distant; petals white, 7.5–10 mm. long, 2–3.5 mm. wide, obovate to oblanceolate, cuneate, attached to the stamens for 1–2 mm., the claw 1.5–2.0 mm. long.

Longistylous form. Stamens 5.9–6.8 mm. long, the filaments united up to the anthers, sometimes very few scattered, simple hairs on the staminal tube, the anthers 1.1–1.4 mm. long, 0.5–0.9 mm. wide, oblong, emarginate at both ends, nearly to the middle from the apex; pistil 6.4–8.1 mm. long, the styles filiform, free for 2–6 mm., to the ovary, or united for 1–3 mm., papillose for 0.7 mm., the ovary globular-ovoid, sericeous, hairs mostly at the apex, sericeous, simple, 0.5–1.7 mm. long, stipe none.

Brevistylous form not seen.

Fruit 3.0–3.5 mm. long, 3.3–4.0 mm. wide, globular, obtusely pentagonal, the sulci between the carpels shallow, extending a fifth to a fourth of way to the center of the fruit, hirsute-tomentose, hairs simple, 0.2–1.5 mm. long; dehiscence first loculicidal all along the dorsal sutures and then along the ventral sutures, finally septicidal, the fruit falling apart; seeds brown, 1.7–2.3 mm. long, 1.0–1.5 mm. wide, 1 per cell.

Flowering specimens collected in January, May to July, October and November; fruiting ones in January, May to July, and November.

TYPE LOCALITY: Ugalla River, W. Tanganyika, type F. Hoffman 275.

DISTRIBUTION: Sierra Leone, Cameroon, Central African Republic, Angola, The Congo, Uganda and Tanganyika, in forest, low grassland swamp, and dry clay soil, at 30–1,216 meters elevation.

SIERRA LEONE: *Thomas* 8101 (US). Yonibana, *Thomas* 4191 (S).

CAMEROON: Bipinde, *Zenker* 1318 (L, S), 4740 (L). SOUTH CAMEROON: Bitye near R. Ja., *Bates* 604 (US).

CENTRAL AFRICAN REPUBLIC: Haut-Oubangui, between the Yambéré and Krébedje, *Chevalier* 6044 (L).

ANGOLA: PORTUGUESE CONGO: Sumba, Peco, near Zaire River, *Gossweller* 8714 (US).

THE CONGO: Kwango, *Vanderyst* 1413 (US). Bangala, *Fr. Hens* C 388 (L). COQUILHATVILLE: Tkenga, *Vebrun* 717 (S). Yangambi, *Louis* 16145 (US).

UGANDA: Kivuru, *Dümmer* 881 (US).

TANGANYIKA: Stromgebiet des Ruhudje, Landschaft Massagati, nördlich des Flusses, ca 35°30′ E., *Schlieben* 1092 (S, US, US neg. 5611).

This species is close to *M. villosa*, *M. mellissifolia*, and *M. splendens*. It differs from the first by having axillary inflorescences rather than predominantly terminal ones. Its flowers are twice as large as the

second and its leaves are larger, often hairier and usually have relatively shorter petioles. It differs from the third by having longer petioles, usually broader leaves, rounded to subcordate at the base rather than cuneate to rounded, higher serrations, longer pedicels, a shorter calyx, and broader petals.

33. Melochia melissifolia Benth. *in* Hook. Journ. Bot. 4:129. 1841.
Melochia concinna Miq. Linnaea 22:467. 1849.
Riedleia concinna (Miq.) Walp. Ann. 2:166. 1852.
Riedleia sparsiflora Klotzsch ex Walp. Ann. 2:166. 1852.

An erect or spreading herb to suffrutex, blooming the first year, sometimes with several slender stems from near the base, 0.08–1.0 meter high, the taproot as thick as the base of the stem, the young stems pilose, hairs stellate and simple, occasionally a few glandular and forked, 0.2–1.0 mm. long, internodes (0.8–) 1.3–3.7 cm. long; stipules 2.6–5.3 mm. long, 0.6–1.0 mm. wide, lanceolate, mostly ciliate, hairs simple, 0.3–1.3 mm. long; petiole 0.2–1.5 cm. long, hirsute-pilose, hairs simple and stellate, 0.2–1.5 mm. long.

Lamina 0.5–3.5 cm. long, 0.5–1.6 cm. wide, ovate to lanceolate, the base rounded, the apex usually acute, sometimes rounded, a few scattered, simple, generally appressed hairs, sometimes a few glandular, 0.3–1.1 mm. long on both surfaces, especially on the veins of the lower surface, the upper surface sometimes glabrate and sometimes reddish, the margin irregularly crenate-serrate, serrations (0.5–) 0.9–2.3 mm. wide, 0.3–1.0 mm. high, 5–8 pairs of primary veins, 2 are basal.

Inflorescences axillary, consisting of 1–5 flowers in the axils of each of the upper 6–19 leaves, 0.5 cm. long, sometimes also terminal at 4 nodes, 4 cm. to first leaf, peduncle none, the pedicel 0–2 mm. long; bracts sometimes united at the base, 3 immediately subtending the flower, longer than the petals, (2–) 3–6.7 (–8.5) mm. long, 0.3–1.1 mm. wide, lanceolate to linear, mostly ciliate, hairs simple, 0.5–1.5 mm. long.

Calyx membranous, 1.4–2.4 mm. long, 1.7–2.8 mm. wide, with a few scattered simple hairs 0.3–1.0 mm. long, the teeth 0.4–1.0 mm. long, 0.4–0.8 mm. wide, deltoid, the sinus obtuse; petals white, pink, or rose lilac, (1.7–) 2.7–4.0 mm. long, 0.5–1.4 mm. wide, obovate-oblanceolate, the claw 0.3–0.5 mm. long, almost entirely free from the staminal tube.

Androecium and gynoecium about equal in length. Stamens (1.2–) 1.7–2.4 mm. long, the filaments free for 0.3–1.2 mm., the anther relatively small, oblong, 0.3–0.4 mm. long, 0.2–0.3 mm. wide, emarginate at both ends, nearly to the middle from the apex; pistil 1.3–2.3 mm. long, the styles free to the ovary, 0.6–1.1 mm. long, the ovary ovoid, densely hirsute-sericeous, hairs 0.3–1.0 mm. long.

Fruit 2.4–2.7 mm. long, 3.2–3.3 mm. wide, subglobose, pentagonal, the sulci between the carpels very shallow, extending a fifth to a fourth of way to the center of the fruit, hirsute, hairs simple, 0.1–1.0 mm. long, stipe none; dehiscence loculicidal along the dorsal suture and then along the ventral, eventually also septicidal, the fruit falling apart; seeds 1.4–1.8 mm. long, 1–1.3 mm. wide, trigonal, dark brown, 1 per cell.

Flowering specimens collected from March to May, and July to January; fruiting ones, from March to July, and September to January.

TYPE LOCALITY: British Guiana, syntypes collected by Schomburgk, no. 366, and French Guiana, syntypes collected by Leprieur, no. 122, one cited below.

DISTRIBUTION: Central America, the Guianas, Brazil, Guinea, Sierra Leone, and the Congo, usually in wet or moist thicket, roadside, weedy fields, savanna, sometimes in dry forest, at 0–850 meters elevation.

BRITISH HONDURAS: *Schipp* 1060 (MICH, S).

COSTA RICA: Boca Culebra, shore of the Pacific, *Pittier* 12056 (US). Boruca, *Pittier* 4573 (US). Mano de Tigre, between Boruca and Térraba, *Tonduz* 4592 (US). SAN JOSÉ: El General, *Skutch* 2881 (S, US).

PANAMA: Paitilla, *Bro. Heriberto* 235 (US). COCLÉ: Aguadulce, *Pittier* 4833 (US). CANAL ZONE: Gamboa, *Standley* 28364 (US). Corozal, *Standley* 27351 (S, US). Summit, *Standley* 26925 (US). Las Cascadas Plantation, near Summit, *Standley* 29629 (US), 30131 (US). Balboa, *Standley* 25520 (US). Hills west of the Canal, near Gatún, *Standley* 27271 (US). Cerro Gordo, near Culebra, *Standley* 26028 (US). COLÓN: Between France Field, Canal Zone, and Cativa1, *Standley* 30384 (US). PANAMÁ: Vicinity of Juan Franco Race Track, near Panamá, *Standley* 27756 (US). Corozal Road, near Panamá, *Standley* 26863 (US). North of Panamá, *Bro. Paul* 586 (US). Río Tecumen, *Standley* 29435 (S, US). Near the big swamp east of the Río Tecumen, *Standley* 26496 (US). Near Matías Hernández, *Standley* 28992 (US). Nuevo San Francisco, *Standley* 30756 (US). Laguna de Portala, near Chepo, *Pittier* 4619 (US).

FRENCH GUIANA: *Leprieur* 122 (US, syntype). Îles du Salut, Mana, *Sagot* 53 (P, S, W), 54 (W). Cayenne, *Aublet* s.n. (W).

SURINAM: *Focke* 31 (L). *Hostmann* 1575 (W). *Tulleken* 242 (L). Near Paramaribo, *Kappler* 1575 (W). Fluv. Cappename Sup., *Boon* 1115 (US). Para, *Splitgerber* 1158 (L).

BRITISH GUIANA: Roraima, *Schomburgk* 265 (W). Mazaruni Station, *Sandwith* 1084 (S).

BRAZIL: *Burchell* 9027 (K). AMAZONAS: Manaus, *Schwacke* 366 Coll. III (R, US). PARÁ: *da Costa* 67A (R, US). Near Pará, *Burchell* 9566 (GH, K, L). Between S. João de Araguaya and S. Anna, *Burchell* 9234 (K). Vicinity of Santarem, *Spruce* May 1850 (RB, W). MATO GROSSO: Cuiabá, *Malme* s.n. (S).

GUINEA: Near Mamou, *Sweeney* 4 (US).

SIERRA LEONE: *Thomas* 6117 (US). Freetown, *W. H. & A. H. Brown* 59 (US).

THE CONGO: WOMBALI: Casier St. Jean Mission, *Vanderyst* 1269 (S).

This species is close to *Melochia manducata* Wright, but the inflorescences are not pedunculate, the fruit and leaves are smaller, and the fruit is not covered with glandular hairs. It is also related to *M. villosa* (Mill.) Fawc. & Rendle but differs in the position of the inflorescences and size of the fruit, and its flowers are not dimorphic.

It is apparently indigenous to America and Africa.

It is illustrated by Schumann (47).

34. Melochia arenosa Benth. *in* Hook. Journ. Bot. 4:127. 1841.

Melochia cinerea St.-Hil. & Naud. Ann. Sci. Nat. II, 18:35. 1842.

Riedleia littoralis Poepp. & Endl. Nov. Gen. & Sp. Pl. 3:73. 1845.

Melochia littoralis (Poepp. & Endl.) Schum. *in* Mart. Fl. Bras. 12(3):44. 1886.

Melochia corumbensis S. Moore, Trans. Linn. Soc. II, Bot. 4:317. 1895.

?*Melochia cinerea* St.-Hil. & Naud. var. *discolor* Hassl. Addenda Pl. Hassl. 12. 1917 (without description).

Melochia llanorum Cuatr. Rev. Acad. Colomb. 8:487. 1952.

A low shrub, sometimes herb, 0.3–2 meters high, the young stems and petioles densely cineraceous-tomentulose, hairs stellate, 0.1 mm. long, also a very few glandular hairs, 0.1–0.2 mm. long, internodes 1–4.3 cm. long; stipules deciduous, 2.6–9.5 mm. long, 0.3–1.0 mm. wide, usually linear-acute, densely tomentulose, hairs stellate, 0.1 mm. long, a few simple hairs, 0.2–1.0 mm. long; petiole 0.2–2.9 cm. long.

Lamina 0.9–7.5 cm. long, 0.6–5.5 cm. wide, ovate, oval, oblong or lanceolate, the base rounded to subcordate, the apex rounded to acute, the upper surface green to canescent, the lower cinereous, both densely tomentulose, velvety to the touch, hairs stellate, with 8–12 rays, 0.1 mm. long, sometimes a few simple hairs 0.2–0.8 mm. long, the margin irregularly crenate-serrate, serrations 0.7–3.8 mm. wide, 0.2–2.5 mm. high, 5–10 pairs of primary veins, 2 are basal.

Inflorescences in axils of upper 3–9 (–25) leaves, 1.3–2.5 cm. long, the ultimate divisions umbellate, 3–6 flowers per umbel, the peduncle 0.3–1.5 cm. long, 1–3 per axil, the pedicel 2–5 mm. long, to 8 mm. long in the fruiting stage; bracts at the base of the pedicels, 1.8–4.3 (–8.0) mm. long, 0.2–1.1 mm. wide, usually linear, densely tomentulose, hairs stellate, occasionally glandular, 0.1 mm. long.

Calyx 3.1–5.5 mm. long, 3.2–5.4 mm. wide, not accrescent, densely tomentulose, hairs stellate, a few glandular, 0.1–0.2 mm. long, the teeth 1.0–2.7 mm. long, 0.5–1.7 mm. wide at the base, nearly linear distally, broadening at the base, the sinus rounded, the teeth distant; petals rich pink, red, rose violet, lilac, lilac or violet with yellow proximally, 6–10 mm. long, 1.8–4.0 mm. wide, obovate, oblanceolate, or oblong, the claw 0.8–1.5 mm. long, the base free from the staminal tube or attached to it for 0.5–1.5 mm.

Longistylous form. Stamens 3.4–4.7 mm. long, the filaments united up to the anthers, sometimes a few stellate hairs 0.1 mm. long near the base of the staminal tube, the anther 1.0–1.3 mm. long, 0.5–0.7 mm. wide, oblong, emarginate at both ends, nearly to the middle from the apex; pistil 4.8–7.0 mm. long, the styles filiform, free for 2.7–4.0 mm., to the ovary or united for 0.6–1.0 mm., papillose at the apex for about 1.2–2.0 mm., the ovary ellipsoid to globular-ovoid, the ovary and base of styles tomentulose-hirsute, hairs 0.1–1.0 mm. long, stipe none.

Brevistylous form. Stamens 5.6–7.7 mm. long, the filaments free for 2.6–4.3 mm., sometimes a few hairs at the base of the tube, sometimes staminodes present, 0.2–0.3 mm. long, the anther 1.1–1.7 mm. long, 0.5–0.8 mm. wide, oblong, slightly emarginate at both ends; pistil 4.8–6.2 mm. long, the styles filiform, free for 1.7–3.8 mm., united for 0.6–0.7 mm., the ovary ovoid, the ovary and base of styles tomentulose, hairs 0.1–1.7 mm. long.

Fruit 3.2–3.5 mm. long, 3.5–4.5 mm. wide, obtusely pentagonal, globose, the sulci between the carpels shallow, extending a fourth to a fifth of way to the center of the fruit, hirsute-tomentulose, hairs simple, forked, and stellate, a very few glandular, 0.1–1.0 mm. long, stipe none; dehiscence loculicidal along entire dorsal and ventral sutures, later septicidal, the fruit falling apart; seeds 2.0–2.3 mm. long, 1.2–1.5 mm. wide, trigonal, dark brown to black, 1 per cell.

Flowering specimens collected from April to July and September to January; fruiting ones, from October to December, April, and June.

TYPE LOCALITY: Syntypes collected by Schomburgk, nos. 31 and 519, the latter cited below, on sandy banks of the Essequibo and Rupununi Rivers, and by Gardner, no. 2489, in Piauí, Brazil, also cited below.

DISTRIBUTION: Cuba and Venezuela to Paraguay, often in places that are sometimes inundated and moist savanna and woods at 130–?1,300 meters elevation.

CUBA: MATANZAS: N. of Matanzas, Hoyo Colorado, *Bro. Alain* 3951 (US).

BRITISH GUIANA: Essequibo and Rupununi Rivers, *Schomburgk* 519 (L, syntype). RUPUNUNI: Lethem, *Irwin* 567 (US). Rupununi Savanna, *Vesey-Fitzgerald* 745 in part (US). BASIN OF THE RUPUNUNI RIVER: Karenambo, lat. 3°45′ N., *A. C. Smith* 2246 (A, K, P, S, US).

VENEZUELA: GUÁRICO: Palo Seco, between La Encrucijada and the Mision de Arriba, Calabozo, *Pittier* 14960 (US).

COLOMBIA: Castañal, *Sonntag* 18 (GH, also US neg. 5612). ARAUCA: Llanos de Casanare, Esmeralda, *Cuatrecasas* 3934 (US, isotype of *Melochia llanorum*, Cuatr.).

BRAZIL: *Regnell* III 631 (P). Western part, *Tamberlik* s.n. (W). AMAZONAS: Amazon Rio, F neg. 9605 ex B, probably an isotype of *Melochia littoralis* (Poepp. & Endl.) Schum. RIO BRANCO: São Marcos, *Ule* 7869 (L). PARÁ: Boa Vista on

the Tapajós River, *Dahlgren & Sella* 65 (US). Jutahy de Almeirim, *Ducke* 18959 (RB). Medio Cuminá, *de Sampaio* 5921 (R, US). Alto Cuminá, *de Sampaio* 5696 (R, US). Rio Erepecurú, *de Sampaio* 5372 (R, US). PIAUÍ: *Gardner* 2489 (US, syntype, also F neg. 9597 ex B in US). MINAS GERAIS: *Claussen* 95 (P, isotype of *Melochia cinerea* St.-Hil. & Naud., also US neg. 5667). MATO GROSSO: Corumbá, F neg. 9601 ex B of *Moore* 905, isotype of *Melochia corumbensis* Moore (US); *Malme* s.n. (S).

PARAGUAY: Alto-Paraguay, Chaco, 21° S. lat., *Fiebrig* 1336 (K, S).

This species can be distinguished from other members of the section by the abundant, very short, stellate hairs with numerous rays (8–12), 0.1 mm. long, on the leaves and by its axillary pedunculate inflorescences.

In addition to the localities cited above, *Schumann* (47) reported *M. arenosa* Benth. from Goiás, *M. littoralis* (Poepp. & Endl.) Schum. from the shores of Lake Ega, Amazonas, Brazil, and *M. cinerea* St.-Hil. & Naud. from Bahia, between Victoria and Bahia, and from upper Surinam. I consider the last two species to be synonyms of *M. arenosa* Benth.

I have not selected a lectotype because I have not seen the syntypes located at Kew.

35. Melochia simplex St.-Hil. Fl. Bras. Mer. 1:164. 1825.

Melochia oblonga Benth. *in* Hook. Journ. Bot. 4:128. 1841.
Melochia sorocabensis Schum. *in* Mart. Fl. Bras. 12(3):42, pl. 8. 1886.
Melochia stricta Schum. *in* Mart. Fl. Bras. 12(3):42. 1886.
Melochia Missionum Ekman, Arkiv. Bot. Stockh. 9(4):47, fig. 10. 1910.
Melochia stricta Schum. f. *Missionum* (Ekman) Hassl. Repert. Sp. Nov. Fedde 8:123. 1910.

An erect or subdecumbent-ascending herb to suffrutex 0.4–1.5 meters high, simple or 2- to 3-branched from near the base, blooming during the first year, the young stems and petioles tomentulose, hirsute or subglabrous, hairs stellate, sometimes also forked, simple, and glandular, 0.1–0.2 (–0.5) mm. long, internodes 0.8–6.9 cm. long; stipules caducous, 2.1–8.0 mm. long, 0.3–1.7 mm. wide, lanceolate to nearly linear, ciliate and sometimes tomentulose, hairs simple, stellate, or forked, 0.1–0.5 mm. long; petiole short, 0.2–1.0 cm. long.

Lamina 1.5–9.5 cm. long, 0.5–3.0 cm. wide, lanceolate to suboblong, nearly linear near the apex of the stem, the base narrowly rounded to slightly cuneate, the apex acute, acuminate, or slightly rounded, the upper surface with few scattered stellate, forked, simple, and rarely glandular hairs, 0.1–0.7 mm. long, the lower surface with scattered hairs or slightly tomentulose, especially on the veins, hairs stellate, a few forked and simple, most 0.1 mm., a few to 1 mm. long, the margin irregularly crenate-serrate, serrations 0.3–6.0 mm. wide, 0.2–1.5 mm. high, 5–12 pairs of primary veins, 1 or 2 are basal.

Inflorescences terminal, extending 1–18 cm. beyond the first leaf, spicate- to paniculate-cymose, the ultimate divisions subcapitate um-

bels of 2–5 flowers, sometimes also or only axillary, 0.8–7.5 cm. long, in the axils of 1–9 leaves, the peduncle 0.2–4.1 cm. long, the pedicel 0.3–3.6 mm. long; bracts 1–5.5 mm. long, 0.1–1.5 mm. wide, deltoid-acuminate, lanceolate, or linear, 2 or 3 immediately subtending the flower or on the pedicel, sometimes in pairs at the base of the pedicel or peduncle, ciliate, a few forked and stellate hairs 0.1–0.5 mm. long on the abaxial surface.

Calyx pale yellowish green, sometimes reddish purple, 2.4–4.5 mm. long, 2.5–5.0 mm. wide, tomentulose or with scattered stellate and sometimes also forked, simple, and glandular hairs 0.1–0.2 (–0.5) mm. long, the teeth 0.7–1.9 mm. long, 0.6–2.2 mm. wide, deltoid at the base to linear at the apex, distant, the sinus rounded to truncate; petals violet, purple, rose, blue, purple distally and yellow proximally, or orange, 5.6–10.2 mm. long, 1.3–4.7 mm. wide, oblanceolate- to obovate-cuneate, free from the staminal tube or attached to it for 0.3–2.0 mm., the claw 0.5–1.5 mm. long.

Longistylous form. Stamens 3.4–4.6 mm. long, the filaments united up to the anthers, the anther 0.9–1.6 mm. long, 0.4–0.7 mm. wide, oblong, emarginate at both ends, nearly to the middle from the apex; pistil 4–5.8 mm. long, the styles filiform, free for 1.6–4.3 mm., united for 0.5–2.8 mm., papillose and subclavate for 0.7–2.0 mm. at the apex, the ovary globular to ovoid, sericeous or hirsute, especially at the apex, hairs simple, 0.2–0.8 mm. long, the stipe 0–0.5 mm. long.

Brevistylous form. Stamens 4.5–6.6 mm. long, the filaments free for 1.7–3.4 mm., the anther 0.9–1.4 mm. long, 0.4–0.7 mm. wide, similar in shape to that above; pistil 3.4–3.6 mm. long, the styles filiform, free for 1.2–1.5 mm., united for 0.3–0.9 mm., the ovary globular to ovoid, sericeous or hirsute, hairs simple, 0.1–1.0 mm. long.

Fruit 3.4–3.7 mm. long, 3.9–4.0 mm. wide, globular, obtusely pentagonal, the sulci between the carpels shallow, extending a fifth to a fourth of way to the center of the fruit, hirsute, hairs simple and sometimes also forked, stellate, and glandular, 0.1–1.1 mm. long, stipe none; dehiscence loculicidal all along the dorsal and ventral sutures, also septicidal, the fruit falling apart; seeds 2.2–2.5 mm. long, 1.1–1.8 mm. wide, trigonal, dark brown, 1 per cell.

Flowering specimens collected from December to April, and in June, August, and October; fruiting ones, from December to March, and in August, and October.

TYPE LOCALITY: The type was collected by St.-Hilaire near the city Guaratingueta, in the northern part of the province of São Paulo, Brazil. The isotype is cited below.

DISTRIBUTION: British Guiana to southern Brazil, Bolivia, Paraguay, and northern Argentina in humid campo, marshes that are often

inundated, among bushes at the edge of a swamp and in shrubby fields, at 160–500 meters elevation.

BRITISH GUIANA: Savannas of the upper Rupununi, *Schomburgk* s.n. (K, type of *Melochia oblonga* Benth., also US neg. 5419).

BOLIVIA: SANTA CRUZ: SARA: Buenavista, *Steinbach* 5483 (GH), 14821 (S).

BRAZIL: F neg. 9608 ex B of *Pohl* 421 (US, presumably the type of *Melochia stricta* Schum.). AMAZONAS: Serra Tayana, *Luetzelburg* 20898 (R). GOIÁS: Brejo do Riacho Fundo, *Glaziou* 20735 (P). Goiás beyond Jaragua, Meia Ponte to Cavalcante, *Burchell* 7821 (P). GOIÁS?: Corgo-Corallinho, *Pohl* 1834 (W). MATO GROSSO: Coxim, *Hoehne* 2990 (R). CORUMBÁ: Fazenda Aguassuzinho, *Pereira et al.* 401 (US). Fazenda Marilândia, *Pereira et al.* 209 (US). RIO DE JANEIRO OR SÃO PAULO: Coralfalza, *Pohl* 314 (W). SÃO PAULO: *Sellow* 5288 in part (R). Near the city Guaratingueta in the northern part of the province, *St.-Hilaire* Cat. No. 756d (P, isotype); F neg. 35385 of the type ex P (US). Mooça, *Brade* 5973 (S). Near Sorocaba, *Riedel & Luschnath* 1994 (LE, isotype of *M. sorocabensis* Schum., also US neg. 5271); *Riedel* 1994 dupl. 19 (P). Atibaia, *George & Liene Eiten* 2404 (US). PARANA: Fóz do Iguaçu, *Hatschbach* 9726 (US). RIO GRANDE DO SUL: S Leopoldo near P. Alegre, *Theissen* (PACA 7554).

PARAGUAY: Border of Rio Tapiracuai at Primavera, *Woolston* 1072 (US). Est. Tagatiya, *Anisits* 2648 (S). Between Rio Apa and Rio Aquidaban, *Fiebrig* 4780=5207 (GH). Road to "Yerbales" montium "Sierra de Maracayu," Jejuigauzu River, *Hassler* 5700 (GH).

ARGENTINA: CORRIENTES: SANTO TOMÉ: Pueblo, *Ibarrola* s.n. (S). MISIONES: Posadas, *Vattuone & Bianchi* 71 (US). Banks of the Alto-Paraná River, *Ekman* 186 (S, type of *Melochia Missionum* Ekman, also US neg. 5614).

This species is related to *Melochia graminifolia* St.-Hil., but the leaves of the latter are linear, rather than lanceolate or oblong, with obscure and considerably fewer serrations.

36. Melochia graminifolia St.-Hil. Fl. Bras. Mer. 1:160, pl. 31. 1825. PLATE 6

Visenia graminifolia (St.-Hil.) Spreng. Syst. 4:Cur. Post. 248. 1827.
Riedleia graminifolia (St.-Hil.) Steud. Nom. II, 2:460. 1841.

An erect perennial herb or suffrutex with 1–3 slender, branched shoots from the base, 0.3–1.2 meters high, 2–4 mm. wide, the root woody, thick, up to 2 cm. wide, the young stems and petioles with scattered stellate hairs about 0.1 mm. long, internodes 0.5–4.7 cm. long; stipules caducous, 2–4.5 mm. long, 0.2–0.4 mm. wide, deltoid-acuminate to acicular, with few hairs about 0.1 mm. long; petiole very short, 0.1–0.3 cm. long.

Lamina 2–9.7 cm. long, 0.2–0.8 cm. wide, nearly linear, the base narrowed, rounded to cuneate, the apex acute, both surfaces green and glabrous, rarely a few hairs on the veins beneath, the margin entire at the base, irregularly and obscurely serrate at the apex, serrations 2–12 mm. wide, 0.2–0.3 mm. high, 4–8 pairs of primary veins, 1 is basal.

Inflorescence terminal, long, slender, branched, racemiform or paniculate, extending 6–31 cm. beyond the first leaf, the flowers soli-

tary or in umbels of 2 or 3, sometimes also in the axils of the upper 1–3 leaves, 2.5–19 cm. long, the pedicels 2–9 mm. long; bracts 0.5–1.5 mm. long, 0.2–0.4 mm. wide, deltoid-acuminate to nearly linear, with few hairs about 0.1 mm. long.

Calyx 1.8–3.0 mm. long, 2.7–4.1 mm. wide, stellate and glandular puberulous, hairs 0.1–0.3 mm. long, the teeth 0.6–1.1 mm. long, 0.4–0.5 mm. wide, deltoid-acute or deltoid-acuminate to nearly linear, the sinus very obtuse, the teeth distant; petals pale lilac, blue, bluish pink, rose, yellowish and red striped at the base, purple distally and yellow with purple veins proximally, violet, yellow, or white, 6.5–10.5 mm. long, 3.0–5.2 mm. wide, obovate-cuneate, the claw 0–0.5 mm. long, the base of petals attached to the staminal tube.

Longistylous form. Stamens 2.6–4.0 mm. long, the filaments united up to the anthers, the anther 1.1–1.2 mm. long, 0.5–0.7 mm. wide, oblong, emarginate at both ends, almost to the middle from the apex, sacs somewhat divergent at the apex; pistil 3.6–4.7 mm. long, the styles free for 1.5–3.1 mm., papillate at the apex for 1.5–2.3 mm., the ovary ellipsoid to ovoid, glabrous or with few hairs 0.1 mm. long, the stipe 0.3–0.8 mm. long.

Brevistylous form. Stamens 5.8 mm. long, the filaments free for 3.0 mm., the anther 1.3–1.4 mm. long, 0.6 mm. wide; pistil 3 mm. long, the styles free for 1.2 mm., the stipe 1 mm. long.

Fruit obtusely pentagonal, depressed-globose, very shallowly sulcate between the carpels, 3.3–4.0 mm. long, 4.2–4.8 mm. wide, tometulose, hairs simple and forked, 0.1–0.2 mm. long, the stipe 0.4–0.8 mm. long; dehiscence loculicidal along the dorsal suture and later septicidal; seeds 2.2–2.5 mm. long, 1.4–1.6 mm. wide, trigonal, black.

Flowering specimens collected from September to July; fruiting ones, from October to January, and March to May.

TYPE LOCALITY: Marshes near the village of S. Domingos, Minas Gerais, Brazil. Type collected by St.-Hilaire, isotype cited below.

DISTRIBUTION: Eastern Colombia to Paraguay, and southern Venezuela and British Guiana to São Paulo, Brazil, usually in wet argillaceous savannas, sometimes dry grassy llanos, and campo, at 70–500 meters elevation.

BRITISH GUIANA: On Rio Branco, *R. Schomburgk* 805 (L, US).

VENEZUELA: BOLÍVAR: La Paragua, *L. Williams* 12582 (US). Rio Paragua, Potrerito, *Cardona*, 696 (US). Rio Paragua, near Chorrera de Aguacanta, *Killip* 37552 (US).

COLOMBIA: META: Rio Meta, La Poyata, 65 km. E. of Villavicencio, *Cuatrecasas* 4473 (US); *Haught* 2518 (US). Rio Guaviare, San José del Guaviare, *Cuatrecasas* 7720 (US). San Juan de Arama, *Idrobo & Schultes* 699 (US).

BOLIVIA: Velasco, *Kuntze* (US).

BRAZIL: RIO BRANCO: Estrada Bôa Vista-Caracaraí, *Black* 51–13509 (US). Fazenda Bom Intento, *Black* 51–14047 (US). MINAS GERAIS: S. Domingos,

St.-Hilaire 1589 (P, isotype, also US neg. 5664). Goiás: *Gardner* 3604 (US). Mato Grosso: Cáceres, *Hoehne* 1119 (R), 604 (R). Cuiaba, *Malme* Regnell II 3271 (S). Porto Murtinho, *Malme* s.n. (S). Rio de Janeiro: Serra da Estrella, Mandioca, *Glaziou* 12459 a (R). São Paulo: Bank of Rio Grande at Melaniros (?), *Regnell* III 279 (S).

PARAGUAY: Between Rio Apa and Rio Aquidaban, Centurion, *Fiebrig* 4123=4029 (L, US). Rio Apa, *Hassler* 7683 (S). In Quebrachal Bco. Branco, *Anisits* 2257 (S).

This species is distinguished from all other species in the genus by its nearly linear, obscurely serrate leaves. It appears to be most closely related to *Melochia simplex* St.-Hil., which has broader leaves and distinct serrations.

37. Melochia manducata Wright *in* Sauvalle, Anal. Acad. Ci. Habana 5:241. 1868.

Melochia glandulifera Standl. Contr. U.S. Nat. Herb. 23:803. 1923.

An erect, annual, simple or branched herb to suffrutex, the stem hollow, 0.3–0.65 meter high, the primary root not as thick as the base of the stem, secondary roots abundant, the young stems glabrous or with a few glandular, stellate, forked, or simple curved hairs 0.1–0.5 mm. long in a narrow longitudinal line, internodes 1.5–6.2 cm. long; stipules 3–7.4 mm. long, 0.7–1.3 mm. wide, lanceolate, ciliate, hairs simple, 0.1–0.7 mm. long; petiole 0.2–5.0 cm. long, tomentulose in a longitudinal line on the upper surface, hairs stellate, forked, a few glandular, 0.1–0.5 mm. long.

Lamina 3–7.5 cm. long, 0.9–6.2 cm. wide, lanceolate to broadly ovate, the base rounded, truncate or subcordate, the apex acute, subglabrous, both surfaces with a few simple appressed hairs 0.1–0.5 mm. long, mostly on the veins, the margin irregularly crenate-serrate, serrations 0.7–3.1 mm. wide, 0.3–1.6 mm. high, 9–12 pairs of primary veins, 2 are basal.

Inflorescences axillary, 0.7–2.8 cm. long, in the axils of the upper 6–10 leaves and sometimes also terminal, extending 1–1.5 cm. beyond the first leaf, umbellate and capitate as well as pedunculate and non-pedunculate in the same axils, 2 or 3 flowers per peduncle, 5–8 flowers per axil, the peduncle 0–1.6 cm. long, the pedicels 0–14.0 mm. long; bracts 2 or 3 immediately subtending the flower, 1.5–5.0 mm. long, 0.3–0.9 mm. wide, lanceolate, ciliate, hairs simple, 0.1–0.5 mm. long.

Calyx membranous, 1.5–2.4 mm. long, 2.3–3.2 mm. wide, with scattered simple and sometimes also a few glandular hairs 0.1–0.2 mm. long, the teeth distant, 0.5–0.8 mm. long, 0.2–0.6 mm. wide at the base, nearly linear toward the apex, the sinus rounded to truncate; petals rose, reddish lilac, or purple, 3.8–4.7 mm. long, 1.3–1.7 mm. wide, obovate to obovate-oblong, free from the staminal tube or attached to it for 0.5 mm., the claw 0.2–0.4 mm. long.

Androecium and gynoecium nearly equal in length. Stamens 2.1–2.4 mm. long, the filaments united up to the anthers, the anther 0.5–0.8 mm. long, 0.3–0.5 mm. wide, oblong, emarginate at both ends, nearly to the middle from the apex; pistil 2.2–2.5 mm. long, the styles filiform, free for 0.8–1.2 mm., united for 0.3 mm., the ovary globular-ovoid, hirsute-tomentulose, hairs simple, 0.1–1.0 mm. long, stipe none.

Fruit 2.7–4.0 mm. long, 3.8–4.8 mm. wide, globular, pentagonal, the sulci between the carpels very shallow, extending a fourth to a fifth of way to the center of the fruit, covered with glandular and simple hairs 0.1–0.7 mm. long, the stipe 0–0.2 mm. long; dehiscence loculicidal along the dorsal and ventral sutures, later septicidal, the fruit falling apart; seeds 1.7–2.3 mm. long, 1.0–1.4 mm. wide, blackish brown, 1 per cell.

Flowering and fruiting specimens collected from October to March, and in August.

TYPE LOCALITY: In palm forest, llanos, and moist places around Huaiquiba, San Cristóbal, Cuba, probable isotypes cited below. I select *Wright* 3510 (US) as lectotype.

DISTRIBUTION: Mexico, Guatemala, Panama, Cuba, Dominican Republic, Colombia, Ecuador, and northern Brazil, in swamp shrubbery, moist places on the road, marsh, llanos, in sandy soil, at 0–100 meters elevation.

MEXICO: GUERRERO: Acapulco and vicinity, *E. Palmer* 107 in 1984–95 (US). CHIAPAS: Tonalá, *Purpus* 6925 (UC; US, type of *Melochia glandulifera* Standl.).

GUATEMALA: Retaluleu, *Bernoulli & Cario* 3114 (K).

PANAMA: PANAMA: Near the big swamp E. of Rio Tecumen, *Standley* 26655 (US).

CUBA: *C. Wright* 3510 (GH, S, US, probably isotypes).

DOMINICAN REPUBLIC: PACIFICADOR: Pimentel, *Abbott* 653 (US). Santo Domingo, Duarte, Matanzas at Rio Boba, *Ekman* 15866 (S).

COLOMBIA: MAGDALENA: Santa Marta, *H. H. Smith* 724 (S, US). SANTANDER: Along Rio Magdalena near Barranca Bermeja, *Molina & Barkley* 18S205 (US). Puerto Wilches and vicinity, *Killip & Smith* 14790 (US).

ECUADOR: Los RIOS: Hacienda Clementina on Rio Pita, *Asplund* 5573 (R, US).

BRAZIL: AMAZONAS: Manaus, Rio Negro, *Ule* 5393 (K, L). PARÁ: Below Obidos, *Kuhlmann* 83 (RB).

This species is close to *M. corchorifolia* L., but differs in that its inflorescences are principally axillary rather than terminal, and are often evidently pedunculate, those of *M. corchorifolia* L. are usually not pedunculate.

38. Melochia lanceolata Benth. *in* Hook. Journ. Bot. 4:128. 1841.
Melochia betsiliensis Baker, Journ. Linn. Soc. 22:451. 1887.

An erect, simple herb, the stem hollow, or branched shrub, the young stems with a narrow longitudinal line of stellate hairs 0.1–0.4 mm. long, glabrous beyond the third internode, internodes (0.7–) 1.5–6.0 cm. long; stipules 1.5–2.2 (–5.0) mm. long, 0.4–0.5 (–1.5) mm. wide, nearly linear or lanceolate, ciliate and with few scattered, simple hairs 0.1–0.2 mm. long; petiole (0.2–) 0.5–3.2 cm. long, slender, with few simple, forked, and stellate hairs 0.2–0.5 mm. long.

Lamina (1.3–) 4.1–10.0 cm. long, 0.6–3.5 cm. wide, lanceolate, the base rounded, the apex acuminate or acute, sometimes obscurely lobed as in *M. corchorifolia* L., subglabrous with very few scattered simple hairs 0.1–0.3 mm. long on the midrib of the upper surface and veins of the lower surface, the margin irregularly serrate, serrations 1–2.7 (–4) mm. wide, 0.3–0.9 mm. high, 9–13 pairs of primary veins, 1 or 2 are basal.

Inflorescence 1–4 cm. long, up to 11 cm. in the fruiting stage, terminal and in the axil of the first leaf, coarctate, corymbiform, the ultimate divisions umbellate, 2 or 3 flowers per umbel, the peduncle 0.5–1.0 cm. long, 2 cm. according to Schumann (47), the pedicel (0.3–) 1.5–4.7 mm. long, with glandular and simple hairs 0.1–0.3 mm. long; bracts usually at the base of the pedicel, 0.5–3.5 mm. long, 0.1–1.0 mm. wide, lanceolate to linear, ciliate with few simple, forked and sometimes glandular hairs 0.1–0.3 mm. long.

Calyx 1.5–2.0 mm. long, 2.0–3.5 mm. wide, with very few simple hairs 0.1 mm. long and glandular ones 0.3–0.6 mm. long, the teeth 0.4–0.5 mm. long, 0.2 mm. wide, linear, distant, the sinus truncate; petals flavescent or lilac, (3.7–) 5.6–6.5 mm. long, (1–) 3–4 mm. wide, obovate-cuneate, attached to the staminal tube for 0.6 mm., the claw 0.2–0.3 mm. long.

Androecium and gynoecium nearly equal in length. Stamens 2.2–2.6 mm. long, the filaments free for 0.2–0.4 mm., the anther 0.6 mm. long, 0.4 mm. wide, oblong, emarginate at both ends, nearly to the middle from the apex; pistil 2.2–2.7 mm. long, the styles filiform, 0.8–1.3 mm. long and free to the ovary, or united for 0.1–0.2 (–0.7) mm., the ovary globular, with few glandular and simple hairs 0.2–0.4 mm. long, stipe none.

Fruit 3.5–4.0 mm. long, 4.0–4.1 mm. wide, globose, very slightly pentagonal, the sulci between the carpels very shallow, extending one-fifth of way to the center of the fruit, with scattered simple and glandular hairs 0.3–0.5 mm. long, the stipe 0.5 mm. long; dehiscence loculicidal along the dorsal and ventral sutures, the fruit falling apart; seeds not quite ripe, 2 mm. long, 1.1 mm. wide, brown, 1 per cell.

Flowering and fruiting specimens collected in May.

TYPE LOCALITY: The type was collected by Schomburgk, no. 362, in British Guiana; an isotype is cited below.

DISTRIBUTION: British Guiana and Surinam, in shallow water, in shade.

SURINAM: *Hostmann* s.n. (L), 449 (W), 457 a (S). *Hostmann & Kappler* 46 (S), 657 B(S). *Schimper* 657 (W). Para, *Splitgerber* 1001 (L).
BRITISH GUIANA: *Schomburgk* 362 (L, isotype).
MADAGASCAR: *Baron* 4757 (P), 4678 (P), syntypes of *M. betsiliensis* Baker.

This species is close to *M. corchorifolia* L., but its inflorescence is corymbiform rather than subcapitate. The leaves of *M. corchorifolia* are most often ovate, those of *M. lanceolata* are lanceolate. Both species are characterized by the nearly equal length of androecium and gynoecium.

39. Melochia corchorifolia L. Sp. Pl. 675. 1753.
Melochia concatenata L. Sp. Pl. 675. 1753; Hook. Fl. Brit. Ind. 1:374. 1874, in synonymy.
Melochia supina L. Sp. Pl. 675. 1753; Hook. Fl. Brit. Ind. 1:374. 1874, in synonymy.
Corchorus javanicus Burm. f. Fl. Ind. 123. 1768.
Melochia cordata Burm. f. Fl. Ind. 143. 1768.
Melochia erecta Burm. f. Fl. Ind. 143. 1768.
Mougeotia corchorifolia (L.) H.B.K. Nov. Gen. & Sp. 5:326, adnot. 1823.
Riedleia concatenata (L.) DC. Prodr. 1:492. 1824.
Riedleia corchorifolia (L.) DC. Prodr. 1:491. 1824.
Riedleia supina (L.) DC. Prodr. 1:491. 1824.
Riedleia radiata Blume, Bijdr. 86. 1825.
Visenia concatenata (L.) Spreng. Syst. 3:31. 1826.
Visenia corchorifolia (L.) Spreng. Syst. 3:30. 1826.
Visenia supina (L.) Spreng. Syst. 3:31. 1826.
Melochia affinis Wall. Cat. no. 1198. 1829.
Melochia pauciflora Wall. Cat. no. 1199. 1829.
Polychlaena ramosa G. Don, Gen. Syst. 1:488. 1831.
Polychlaena simplex G. Don, Gen. Syst. 1:488. 1831.
?*Geruma subtriloba* Blanco, Fl. Filip. 182. 1837.
Lochemia corchorifolia Arn. Ann. Sc. Nat. sér. 2. 11:172. 1839.
Hibiscus donii Walp. Rep. Bot. Syst. 1:304. 1842.
Hibiscus endlicheri Walp. Rep. Bot. Syst. 1:304. 1842.
Melochia Burmanni Zoll. & Mor. Syst. Verz. Zoll. 27. 1846.
Melochia longebracteolata J. Ar. *in* Mém. Inst. Sci. Madag., sér. B. 7:66. 1956.

An annual herb or perennial subshrub, sometimes gregarious, simple or branched, erect or decumbent, a few centimeters to 2.5 meters long, the taproot not thicker than the base of the stem, the young stems sometimes hollow, with scattered stellate hairs sometimes also forked and simple, 0.1–0.7 mm. long, and also sometimes hairs in longitudinal lines about 0.5 mm. wide, internodes 2–10 cm. long; stipules 3–9 mm. long, 0.5–1.5 mm. wide, deltoid-acuminate to lanceolate-ovate, mostly ciliate, hairs mostly 0.3–1 mm. long; petiole 0.3–2.0 (–6.0) cm. long.

Lamina green, sometimes purplish, (1.0–) 2–6 (–9.8) cm. long, (0.5–) 1–2.6 (–7.0) cm. wide, ovate to lanceolate, the base usually rounded, sometimes truncate, the apex acute, both surfaces subglabrous, usually a few simple hairs 0.1–0.8 mm. long on the midrib of the upper surface and on the midrib and veins of the lower surface, the margin irregularly crenate-serrate, serrations 1–4.2 mm. wide, 0.5–1.0 mm. high, 6–10 pairs of primary veins, 2 are basal.

Inflorescence terminal, 1–2 cm. long, 0.5–3.5 cm. wide, subcapitate, rarely radiately grown out to 3 cm., consisting of about 5–25 often fragrant flowers, also sometimes at apices of branches, and rarely 1 or 2 flowers in the axils of the upper 3–5 leaves, the pedicels 0–3 mm. long; bracts 3.9–7.5 mm. long, 0.3–1.9 mm. wide, 3 or 4 immediately subtending the flower and usually 2 more below, ovate-lanceolate to nearly linear, mostly ciliate, hairs 0.2–1.0 mm. long.

Calyx pale green, 2.0–2.7 mm. long, 2.4–3.3 mm. wide, hirsute, hairs simple, 0.2–0.8 mm. long, the teeth 0.4–0.7 mm. long, 0.3–0.6 mm. wide, deltoid-acute, distant, the sinus obtuse; petals white to pink, pink or white distally and yellow proximally, rarely yellow, purple or violet 4.7–6.5 mm. long, 1.2–2.5 mm. wide, obovate to oblanceolate, almost entirely free from the staminal tube or attached to it for 0.8–0.9 mm., the claw 0–0.5 mm. long.

Androecium and gynoecium about equal in length. Stamens 2.4–3.2 mm. long, the filaments white, yellow, or green, united up to the anthers or free for 1 mm., the anther yellow, 0.6–1.0 mm. long, 0.3–0.6 mm. wide, oblong, emarginate at both ends, nearly to the middle from the apex; pistil 2.5–3.2 mm. long, the styles white or green, 1.0–1.5 mm. long, free for 0.9–1.5 mm., usually to the ovary, sometimes united for 0.4–0.6 mm., papillose for most of their length, the ovary ovoid, densely hirsute, hairs simple, 0.5–1.0 mm. long, stipe none.

Fruit green, white, pink, black, or purplish, (3.3–) 4–5 mm. long, (3.6–) 4.5–5.5 mm. wide, globular, pentagonal, the sulci between carpels very shallow, hirsute, hairs simple, 0.3–0.6 mm. long, stipe none; dehiscence first loculicidal along the dorsal suture, then along the ventral suture, eventually also septicidal, the fruit falling apart; seeds 2.2–3.2 mm. long, 1.4–1.8 mm. wide, trigonal, blackish brown.

Flowering and fruiting specimens collected throughout the year but especially in late summer and fall.

TYPE LOCALITY: "Cosmop. trop." The type is in the Dillenius herbarium at Oxford University. There are two specimens in the Linnaean herbarium attributed to *Melochia corchorifolia*. The one labeled by Sir James E. Smith is *M. corchorifolia*; the other, labeled *Melochia corchorifolia* by Solander and *M. nodiflora* by Smith is *M. nodiflora*.

DISTRIBUTION: Old World tropics and subtropics, introduced in the New World. It occurs as a weed in cultivated ground, in open pineland, meadows, and in waste ground, in wet or dry sandy or clay soil, mostly at 0–250 (–1,000) meters elevation.

UNITED STATES: SOUTH CAROLINA: GEORGETOWN: Georgetown, *Godfrey & Tryon, Jr.* 1678 (US). BEAUFORT: Bluffton, *Mellichamp* s.n. (US). GEORGIA: Altamaha River, *Curtiss* 400** (MICH, US). MCINTOSH: Sapelo Island, *Duncan* 20477 (US); *McAtee* 3306 (US). FLORIDA: DUVAL: Jacksonville, *Curtiss* 6511 (US). LEE: Vicinity of Fort Myers, *J. P. Standley* 385 (US). FRANKLIN: Apalachicola, *Chapman* 4206 (US). ALABAMA: MOBILE: Mobile, *Curtiss* 6512 (US). *Mohr* s.n. (US). MISSISSIPPI: HARRISON: Biloxi, *Tracy* 4493 (MICH, US). LOUISIANA: ST. TAMMANY: Covington, Fairview, *Arsène* 11428 (US). JEFFERSON DAVIS: Lake Arthur, *Wise* s.n. (US). TEXAS: ?CHAMBERS: Stowall (?Stowell), *Hanson* 8 (US). HARRIS: Houston, *Thurow* 14 (US). LIVE OAK: George West, *Shiller* 814 (US).

PANAMA: San José Island, Pearl Archipelago, goat farm near Rio Mato Puerco, *Erlanson* 189 (US).

BRAZIL: RIO DE JANEIRO: Environs of Rio de Janeiro and D'Ouro Preto, *Glaziou* 14518 (K). RIO GRANDE DO SUL: Gravatai near P. Alegre, *Capparelli* (PACA 48235).

CONGO: Kitobola, ?*Flamigri* 135 (S). Eala, *Corbisier* 1053 (S)?. Wangota, around Coquilhatville, *Verbrun* 921 (S). Dolo, *Schlechter* 12498 (L). Lutète, *Fr. Hens* A. 280 (L). Yangambi, *Louis* 10626 (US).

KENYA: KWALE: Kivumoni, near Shimoni, *Drummond & Hemsley* 3928 (S).

TANGANYIKA: Dar-es-Salam, *Stuhlmann* 7582 (US). Lutamba See, 40 km. W. of Lindi, *Schlieben* 5372 (S).

ZANZIBAR: *Hildebrandt* 1132 (L).

NYASSALAND: *Buchanan* 73 (US). Nyassa highland, Station Kyimbila, *Stolz* 2026 (L, S).

MADAGASCAR: *D'Alleizette* 818 in part (L). Nossi-Bé, Ambanja, Mahilaka, *Waterlot* 248 (P) type of *M. longebracteolata* J. Ar.

INDIA: *Wight* 240 (L). *Koenig* (S). Malabar Concan Vc., *Stocks* (Herb. Hooker & Thomson Ind. Or.) (L). Simla, ?*D. J. Yaclar* 21 (US). Jalor (Dschalor), *Vaughan* 592 (L). Mysore, *W. B.* 601 (L). Maisur and Carnatic, *G. Thomson* (S). BENGAL: *Hooker & Thomson* (L). *Sulp. Kurz* (US). Calcutta and vic., *Helfer* 73 (L, S, US); *Wallich* 1196/D (L); *Voigt* collectors in 1834–41 (US). ASSAM: *Col. Jenkins* (L, US). TIRAP RIVER VALLEY: 12.4 mi. mark on Ledo Road, *Steinacker* U.S. Amer. Typhus Comm. 6 (S, US). TIRAP-NAMCHIK DIVIDE: 15.4 mi. mark on Ledo Road, *Juan* U.S. Amer. Typhus Comm. 320 (US). NAMCHIK RIVER VALLEY: 21 mi. mark on Ledo Road, *Juan* U.S. Amer. Typhus Comm. 523 (US).

UPPER BURMA: MYITKYINA REGION: Camp Landis area, *Juan* U.S. Amer. Typhus Comm. 120 (S, US).

BURMA and MALAY PENINSULA: Herb. of late East India Co. 620 (L). *Spiff* 620 (S).

THAILAND: SE. PART: Sriracha, *Mrs. Collins* 1880 (US).

MALAYA: SELANGOR: Kanching, Tin mines, *Nur* Singapore field no. 34419 (L, US). MALACCA: *Griffith* s.n. (L); Fish Culture Research Station, *Shah* 12 (L). JOHORE: Kg. Selantai, Mersing, *Burkill & Shah* 2503 (L). SINGAPORE: Nee Soon village, *J. Sinclair* s.n. (L).

INDOCHINA: Trian near Bienhoa, *Evrard* 57 (S), 64 (S). CAMBODIA: Pnompenh, *Godefry* 54 (L). TONKIN: Long-Tchéou, *Simond* s.n. (S).

CHINA: HAINAN: CHING MAI: Ku Tung village: Pak Shik Ling, *C. I. Lei* 750 (US), 798 (L). NGAI: Ko Leng, *Lau* 572 (US). KWANGSI: NORTHERN PART: Kwei-lin: San-min village, *Tsang* 28029 (US); Ta-chiang-yuan village, *Tsang* 28258 (US). KWANTUNG: Canton, *Levine* 1633 (US). YANG SHAN: Yang Shan (S. of Linchow), *Tsui* 624 (US). TAPU: Tung Kao Shan, *Tsang* 21732 (S). FORMOSA: *Oldham* 53 (S). Takow, *Henry* 2037 (US). KIANGSI: KIENAN: Sai Hang Cheung, *Lau* 4267 (S, US). CHEKIANG: Tien Mo Shan, *Ching* Herb. U. Nanking 9081 (US). ANHWEI: Wu Yuan, *Ching* Herb. U. Nanking 8942 (US). HUPEH: *Henry* 2315 (US).

SUNDA ISLANDS: SUMATRA: *Junghuhn* 568 (L). Atjeh, Kp. Sigleng, N. van Troeman, *Asdat* 155 (L). Lampong Estate Wai Lima, ?*Sloet* 332 (L), 460 (L). Taloe, *Bünnemeyer* 192 (L). Djambi, S. Lesing, *Posthumus* 973 (L). NORTHERN SUMATRA: Medan, *Lörzing* 13045 (L); Balige to Toba Lake, *Lörzing* 14796 (L). PADANG AND BEDAGEI: Plantation Badjalinggi, *Lörzing* 15204 (L). WEST COAST: Pajakoemboeh, *Stomps* s.n. (L); Koerintji, *Bünnemeyer* 7994 (L). W. K. G. Lago, *Bünnemeyer* 3677 (L); Padang Si Dimpoean: Padang Lawas: Tapianoeli, *Toroes* 4447 (US). EAST COAST: ASAHAN: Tandjoeng Balei, *Hamel* 1097 (S); Padang boelan, *Stomps* s.n. (L); ASAHAN: Rantau Parapat, Bila, *Toroes* 1765 (L), 1556 (US); Aer Kandis (formerly Radja Mas), *Toroes* 2424 (US); Sigamata, *Toroes* 2879 (US). SOUTHERN SUMATRA: Palembang, *Monod de Froideville* 554 (L); Pladjoe, *Rutter-Kooistra* 10 (L); BANKA: Soengei Liat, *Bünnemeyer* 1943 (L). LINGGA ARCHIPELAGO: *Bünnemeyer* 6818 (or 8187). RIOUW ARCHIPELAGO: *Bünnemeyer* 6033 (L). JAVA: *Houwink* 973 (L), 1098 (L). *Zollingero* s.n. (L). *Junghuhn* s.n. in part (L). Tanch Soereal, *Raap* 476 (L). Pasoeroean, *Kobn* ? s.n. (L). Madjinang, *Backer* 18702 (L). Kedoe Karangbolong, *Koorders* 29722 β (L). Depok, *Hallier* s.n. (L). Priok near Jakarta Canal, *Raap* 376 (L). Bogor and vic., *Hallier* 33 (L), 35a, b, c (L); *Hasselt* s.n. (L); Kampong Nangrang, *Schiffner* 2223 (L). Boerlage, *Tjiomas* s.n. (L). Bantardjaja estate, 18 km. S. of Rangkasbitung, *Buwalda* 2868 (L). PREANGER: C. Ploem, (L). Banjoemas and vic., *Kient* 1588 (L), 2694 (L), 3423 (L); *Brinkman* 587 (L); *Koorders* 22129 β (L). Semarang, *Karta* 218 (L); *Koorders* 24862 β (L). Djapara, *Koorders* 29722 β (L). Pekalongan Soeba, *Koorders* 27456 β (L). Bawean Island, *Coert* 1407 (L). MADOERA: Bangkalan, *Backer* 19023 (L). BORNEO: Poeloe-lampei, *Korthals* s.n. (L). *Dachlan* 2422 (L). NORTH BORNEO: *Yates* 72 (US). Tamu Darat at mi. 7 on the Kota Belud, Ranau Road, *Darnton* 55 (L). SARAWAK: *Purseglove & Lundu* P. 4515 (L). CELEBES: Lasao, Eurekang, *Kjellberg* 1177 (S), 3897 (S). Bonto-Parang, *Bünnemeyer* 10556 (L). Pampanoea, *Noerkas* 78 (?75) (L), 74 (L). Menado, Gorontalo, ?*V. Gorontalo* 33a (L).

PHILIPPINES: MINDANAO: COTABATO: Marbel, Ala Valley, *Santos* 4863 (L, US); Buluan, Buluan Marsh, Barrio Siling, *Santos* 5956 (L, US). BUKIDNON: Vic. of Tanculan, *Fénix* B.S. 26003 (L, US); Bugcaon, *Cid* 24 (L). DAVAO: Davao, *De Vore & Hoover* 188 (US), *Copeland* 541 (US); Santa Cruz, *De Vore & Hoover* 238 (US), *R. S. Williams* 2755 (US). SIARGAO: *Ramos & Pascasio* B.S. 34898 (L). NEGROS: Mt. Katugasan, NW. slope of Canlaon Vol., *Edaño* 7648 (L). CULION: *Merrill* 537 (US). MINDORO: Vicinity of San José, *Lambert & Brunson* 108 (US). LUZON: San Miguel, *Hallier* s.n. (L). CAMARINES NORTE: Paracale, *Ramos & Edaño* B.S. 33625 (L). Manila, Quezon City, and vic., *Andersson* s.n. (S), *Rogerson* 1026 (US), *Merrill* 3432 (US), *Steiner* 662 (L, US), *Layosa* 71 (L). LAGUNA: Los Baños, U.S. Explor. Exped. under Capt. Wilkes (US). RIZAL: *Ramos* 1978 (L), B.S. 13554 (S). Bosoboso, *Ramos* B.S. 1469 (US), U.S. Cemetery Camp McKinley, *Steiner* 721 (L, US). UNION: Bauang, *Elmer* 5603 (US). BATAAN: Lamao River, Mt. Mariveles, *Borden* For. Bur.

1917 (US). QUEZON: Alabat Island, *Ramos & Edaño* B.S. 48000 (S). TAYABAS: Atimonan, *Whitford* 635 (US). SORSOGON: Irosin (Mt. Bulusan), *Elmer* 14495 (L, S, US). BULACAN: Angat, *Merrill* Species Blancoanae 325 (US). MOUNTAIN: Benguet, *Loher* 2029 (US). Central Luzon: *Loher* 154 (US).

MOLUCCAS: WETAR: *Bloembergen* 3631 (L). HALMAHEIRA: Kan, Kp. Koesoe, *Nedi* 462 (L). S. peninsula, Weda, *Anang* 442 (L). AMBOINA (AMBON): *Robinson* 1764 (L, US).

NEW GUINEA: Stephansort, *Nyman* 130 (S), *Lewandowsky* 56 (L). Cyclops Mts., along path to Netar, *Dreis* 142 (L). Merauke, *Verstug* 1926 (L). Finschhafen, *Weinland* 246 (L, US). Noord, *Atasrip* 202 (L). PAPUA: Koitaki *Carr* 12682 (L). NORTHERN DIV.: Near Gwaiari village, *Hoogland* 3669 (L, US). WESTERN Div.: Dagwa, Oriomo River, *Brass* 5958 (US); DARU ISLAND: *Brass* 6340 (L). CENTRAL DIV.: NAKEO: Baroka, *Brass* 3698 (L, US).

AUSTRALIA: NORTHERN QUEENSLAND: Townsville, *White* 8967 (US).

SOLOMON ISLANDS: BOUGAINVILLE: Karngu, Buin, *Kajewski* 2279 (L, S, US). GUADALCANAL: Vic. Tenam River and the sea, *Riley* 42 (US).

CAROLINE ISLANDS: Ponape, *Hallier* s.n. (L).

MARIANAS ISLANDS: GUAM: *Thompson* Guam Exp. Sta 240 (US).

JAPAN: KYUSHU: Kawaminami in Hyuga, *Togasi* TNS. 1429 (US). OHSUMI: Koneshime-mura, *Kawagoe* Nov. 5, 1917 (US).

This species is characterized by its subcapitate terminal inflorescence and nondimorphic flowers.

I dissected a flower from the type specimen of *M. longebracteolata* J. Ar. The petals were separate and some of the bracts were shorter than the petals. I have seen a range of hairiness in *M. corchorifolia*. Arènes considers union of petals, bracts longer than the petals, and hairiness of the bracts to be distinguishing characters of his species.

Section IV. *Pyramis* A. Goldberg, nom. nov.

Section *Eumelochia* Griseb. Fl. Brit. W. Ind. 93. 1859.

Perennial, sometimes annual, herbs to shrubs, 0.08–5.0 meters high, the root sometimes 2–5 times thicker than the base of the stem and 0.5–1.3 cm. wide, the young stems often canescent, sometimes glabrate, hairs usually stellate, sometimes simple or forked, sometimes tan, 0.1–1.6 mm. long, internodes 0.2–10 cm. long; stipules 1.5–9.0 mm. long, 0.2–3.7 mm. wide, deltoid-acute or deltoid-acuminate, lanceolate or linear, usually tomentulose and ciliate, hairs simple and usually also stellate and forked, 0.1–2.0 mm. long; petiole 0.1–5.1 cm. long.

Lamina 0.6–12.7 cm. long, 0.3–7.7 cm. wide, usually lanceolate to ovate, obovate or oval, the base rounded to cordate, or cuneate, the apex acute or rounded, rarely acuminate, the upper surface glabrous, hirsute, or tomentose and canescent, hairs stellate, forked or simple, 0.1–2.0 mm. long, the lower surface glabrous to tomentulose and canescent and woolly, hairs usually stellate, sometimes also forked and simple, rarely a few glandular, 0.1–1.6 mm. long, the margin irregularly crenate-serrate, serrations 0.7–7.0 mm. wide,

0.2–2.6 mm. high, 4–12 pairs of primary veins, usually 2 are basal.

Inflorescences usually leaf-opposed, sometimes also axillary, terminal or 90° from the leaf, 1–7 cm. long, the flowers in umbels, sometimes subcapitate, the peduncle (0–)0.1–4.0 cm. long, rarely with a primary branch 0.3–1.1 cm. long, the pedicel 1–7 mm. long; bracts 0.5–6.5 mm. long, 0.1–1.2 mm. wide, similar in shape and pubescence to the stipules.

Calyx 3.7–10.2 mm. long, 2.1–7.0 mm. wide, often tomentulose and canescent, sometimes ciliate and hirsute, hairs stellate, usually also forked or simple, 0.1–2.0 mm. long, the teeth 2.0–7.8 mm. long, 0.6–2.3 mm. wide, the sinus usually acute, sometimes narrowly rounded; petals purple, purple distally and yellow orange proximally, rose, red, violet, blue, white, or yellow, 6.0–15.5 (–17) mm. long, 1.5–5.2 (–5.7) mm. wide, usually obovate or oblanceolate, cuneate or spatulate, attached to the staminal tube for 1–5 mm., the claw 0.6–4.0 mm. long, often with scattered glandular hairs 0.05 mm. long.

Anther 0.7–2.0 mm. long, 0.4–1.0 mm. wide, oblong, slightly emarginate at both ends; staminodes rarely present, 0.1–0.2 mm. long.

Longistylous form. Stamens (2.6–) 3.5–7.0 (–9.0) mm. long, the filaments free for 0.7–3.0 mm.; pistil 4.3–10.9 (–12) mm. long, the styles free for 2–6.7 mm., united for 0.5–4.0 mm., papillose for 0.5–1.5 mm. at the apex.

Brevistylous form. Stamen 5.7–11.3 mm. long, the filaments free for 2.5–7.5 mm.; pistil 3.7–6.9 (–8.0) mm. long, the styles free for 1.4–4.0 mm., rarely free to the ovary, united for 0.5–3.0 mm., papillose for 0.3–1.0 mm. at the apex.

Fruit large, 5–10.5 (–12) mm. long, 3.8–17.0 (–22) mm. wide, pentapterous, usually pyramidal, rarely ovoid, usually rostrate and with acute, acuminate, or rounded lateral angles, the sulci between the carpels deep, extending (one-fourth to) one-third to half way to the center of the fruit, sometimes the base narrowing into a stipe 0.5–1.5 mm. long, tomentulose or hirsute-tomentulose, sometimes canescent, or subglabrous, hairs stellate, sometimes also forked, rarely also simple, 0.1–1.3 mm. long; dehiscence loculicidal all along the dorsal and ventral sutures, eventually also septicidal, rarely tardily dehiscent; seeds 1.7–3.0 mm. long, 1.1–2.0 mm. wide, trigonal, brown, 1 or 2 per cell.

Flowering and fruiting period usually long, sometimes throughout the year.

LECTOTYPE: *Melochia pyramidata* L.

DISTRIBUTION: Texas and Florida to Argentina, West Indies, one species adventive in tropic and subtropic regions throughout the world, usually in open disturbed, usually dry, sometimes wet, areas, at 0–2,500 meters elevation.

40. Melochia hermannioides St.-Hil. Fl. Bras. Mer. 1:163, pl. 32. 1825.
Melochia parvifolia H.B.K. f. *roseiflora* Schum. & Hassl. pro parte. (Hassler no. 6402) Bull. Herb. Boiss. II, 4:70. 1903.
Melochia lacinulata Schum. & Hassl. Bull. Herb. Boiss. II, 4:69. 1903.
Melochia hermannioides St.-Hil. var. *lacinulata* (Schum. & Hassl.) Hassl. Repert. Sp. Nov. Fedde 8:122. 1910.
Melochia hermannioides St.-Hil. var. *lacinulata* (Schum. & Hassl.) Hassl. f. *heterophylla* and f. *typica* Hassl. Repert. Sp. Nov. Fedde 8:122. 1910.
?*Melochia hermannioides* St.-Hil. var. *lanceolata* Hassl. Repert. Sp. Nov. Fedde 8:122. 1910.

A procumbent or decumbent trailing subshrub or perennial herb 0.1–0.5 meter long with several (5–8) slender stems from the base, the root 2½ to 3 times thicker than the stem, the young stems and petioles hirsute-tomentose with short stellate hairs and simple curved hairs 0.1–0.3 mm. long and forked, and straight simple hairs 1.0–1.6 mm. long, internodes 0.5–2.8 cm. long; stipules 2.2–6.5 mm. long, 0.3–1.0 mm. wide, lanceolate to linear, mostly ciliate, hairs simple, 0.2–1.2 mm. long; petiole 0.2–1.7 cm. long.

Lamina 0.9–2.1 cm. long, 0.6–1.4 cm. wide, ovate, sometimes also obovate or nearly orbicular, the base rounded to cuneate, the apex rounded, the upper surface with rather sparse simple, and sometimes also forked and stellate appressed hairs 0.2–1.5 mm. long, the lower surface similarly pubescent, stellate hairs sometimes predominant, hairs 0.2–1.2 mm. long, the margin crenate or crenate-serrate, crenations 1.0–2.6 mm. wide, 0.5–1.9 mm. high, the base entire, 4–6 pairs of primary veins, 1 or 2 are basal.

Inflorescences terminal, rarely also leaf-opposed, 1–3.2 cm. long, the ultimate divisions umbellate, 5–8 flowers per umbel, the peduncle 0–2.2 cm. long, rather slender, the pedicel 1–3 mm. long; bracts 2.0–6.0 mm. long, 0.2–0.6 mm. wide, linear to lanceolate-linear, mostely ciliate, hairs simple, 0.5–1.2 mm. long.

Calyx 5.5–8.2 mm. long, 3.1–4.8 mm. wide, hirsute and ciliate, hairs mostly simple, sometimes also forked and stellate, 0.2–1.5 mm. long, the teeth 4.2–5.6 mm. long, 1.2–2.0 mm. wide, deltoid-acuminate, the sinus acute; petals rose, blue, reddish violet, purple, or violet, rarely white, 8.4–12.8 mm. long, 2.0–4.9 mm. wide, oblanceolate-obovate-cuneate, attached to the stamens for 2.0–3.5 mm., the claw 1–3 mm. long.

Longistylous form. Stamens 5.7–6.0 mm. long, the filaments free for 1.4–2.0 mm., the anther 1.2–1.6 mm. long, 0.6–0.8 mm. wide, oblong, slightly emarginate at both ends; pistil 8.6–9.4 mm. long, the styles filiform, free for 4.2–5.1 mm., united for 1.6–2 mm., papillose for 1–1.5 mm., the ovary narrowly elliptic-ovoid, the ovary and styles up to 1 mm. of the apex covered with stellate, forked, and simple hairs 0.1–1.3 mm. long.

Brevistylous form. Stamens 7.5–8.7 mm. long, the filaments free for 5.0–5.5 mm., the anther 1.3–1.6 mm. long, 0.7–0.8 mm. wide; pistil 4.2–5.2 mm. long, the styles free for 1.5–1.8 mm., filiform, papillose for 0.5–0.8 mm., the ovary narrowly ovoid, pentagonal, hairs on the ovary and styles forked and stellate, 0.3–1.4 mm. long, stipe none.

Fruit 5.0–7.0 mm. long, of which the rostrum is 1.0–2.0 mm. long, 5.0–6.0 mm. wide, pentapterous, pyramidal, the lateral angle of the wings rounded to subacute, points above the middle of the fruit, the sulci extending a fourth to half way to the center of the fruit, pubescence stellate, forked, and simple, hairs 0.1–1.2 mm. long, the longer ones forked and simple, stipe none; dehiscence tardily loculicidal along the dorsal suture and somewhat septicidal; seeds not quite ripe, 2.4–2.9 mm. long, 1.4–1.7 mm. wide, trigonal, obovate, brownish.

Flowering and fruiting specimens collected from September to March.

TYPE LOCALITY: Province of Misiones, Argentina, in herbaceous fields. Type collected by St.-Hilaire, Cat. C_2 no. 2643; isotype cited below.

DISTRIBUTION: Bolivia to Argentina in dry clay campo, sandy herbaceous fields, on hills, at 150–2,500 meters elevation.

BOLIVIA: TARIJA: Padcaya, *Fiebrig* 2536 (L, S, US).

PARAGUAY: Cordillera de Villa-Rica, *Hassler* 8738 (K). Vicinity of Caaguazú, *Hassler* 8899 (K, S). Near Arroyo Primero (Apa), *Hassler* 8450 (S, type of *M. lacinulata* Schum. & Hassl.). Loma nördlich der Cordillera de Altos, *Fiebrig* 935 (K, L, US). Capilla Duarte near Villa-Rica, *Balansa* 2657 (K). Trinidad near Asuncion, *Rojas* 1789 (S). Est. Armonia, *Anisits* 1875 (S). Paraguarí, *Grosse* A3575 (S), A3845 (S). Hiaty, *Jorgensen* 3915 (S, US). Near Tobaty, *Hassler* 6402 (S). ? Itapé, *Jorgensen* 4477 in part (S). Centurion, between Rio Apa and Rio Aquidaban, *Fiebrig* 4207 (L).

ARGENTINA: JUJUY: HUMAHUACA: La Soledad, *Venturi* 8784 (US). SALTA: *Wall* 12 (S). Salta City, N. Caseros, *Sparre* 1184 (S). FORMOSA: Colonia Clorinda, *Venturi* 9150 (US). CÓRDOBA: San Roque, *Hunziker* dupl. 7067 (S). CORRIENTES: MBURUCUYÁ: Est. Sta. Maria, *Pedersen* 510 (S, US). SANTO TOMÉ: Gob. Virasoro, *Ibarrola* 1289 (S). MTE. CASEROS: Mocoretá, *Ibarrola* 2394 (S). MERCEDES: Justino Solaricercainas, *Ybarrola* 2633 (UC). MISIONES: *St.-Hilaire* Cat. C_2, no. 2643 (P, isotype, also US neg. 5668). Posadas, Bonpland, *Ekman* 185 (S).

This species is characterized by its relatively small leaves with relatively large crenations, and by its small capsules. It is similar to *M. parvifolia* H.B.K., but the latter is an erect shrub 0.5–3 meters high with somewhat canescent young stems, and the serrations of the leaves are about a third to half as high as those of *M. hermannioides*. It is also similar to *M. anomala* Griseb., but the latter generally has larger, more densely hairy leaves and shorter peduncles (0–0.3 cm.).

Schumann (47) placed this species in the section *Mougeotia*, and in his key to the species he claimed that the inflorescence is axillary. However, the fruit is pyramidal and the inflorescence is in part leaf-opposed as in the section *Pyramis;* in the section *Mougeotia*, the fruit is subglobose and the inflorescence is axillary rather than leaf-opposed.

Hassler (23) described two varieties of *M. hermannioides:* The type of variety *lanceolata* Hassl. is Fiebrig 4207, collected at Centurion, Paraguay; the type of variety *lacinulata* (Schum. & Hassl.) Hassl. is Hassler 8450, collected near Arroyo Primero (Apa), and cited above. The variety *lanceolata* differs from the type of the species in having lanceolate leaves. I have not seen the type of this variety and withhold judgment as to whether it is distinct. I do not consider the type of the other variety to differ appreciably from the isotype of the species.

41. Melochia parvifolia H. B. K. Nov. Gen. & Sp. 5:325. 1823.

An erect or spreading, branched herb to shrub 0.5–3.0 meters high, the young stems and petioles somewhat canescent, hirsute-tomentulose-villous, hairs stellate, 0.2–1.0 mm. long, internodes 1.0–7.5 cm. long; stipules 2–4 mm. long, 0.4–0.9 mm. wide, deltoid-acuminate, lanceolate or nearly linear, hirsute to tomentulose, ciliate, hairs stellate, forked, and simple, 0.1–1.0 mm. long; petiole 0.1–1.3 cm. long.

Lamina relatively small, 0.6–4.5 cm. long, 0.3–2.8 cm. wide, obovate to elliptic, rarely ovate, the base cuneate or rounded, the apex rounded, the upper surface green, glabrous, subglabrous or tomentulose, hairs simple, forked, and stellate, usually 0.1 (rarely a few to 0.8) mm. long, mostly between the veins, the lower surface green, hirsute to tomentulose, hairs mostly on the veins, stellate and forked, 0.1–0.6 mm. long, puberulous between the veins, hairs 0.1 mm. long, the margin irregularly crenate-serrate, serrations 0.7–3.0 mm. wide, 0.2–1.0 mm. high, 4–7 pairs of primary veins, usually one is basal.

Inflorescences leaf-opposed, 1.3–3.8 cm. long, rarely also terminal, clusters at the upper 2–8 nodes, 3–20 flowers per cluster, umbellate-subcapitate, the peduncle 0.1–1.7 cm. long, 0.6–1.0 mm. wide, rarely branched, the pedicel 1–4 mm. long; bracts 1–4 mm. long, 0.2–0.5 mm. wide, deltoid-acuminate, lanceolate or linear, hirsute to tomentulose, ciliate, hairs simple and stellate, 0.2–0.8 mm. long.

Calyx 5.0–9.5 mm. long, 3.7–5.6 mm. wide, hirsute to tomentulose, ciliate, hairs forked, simple, and stellate, 0.1–1.0 mm. long, the teeth 3.3–5.0 mm. long, 1.2–1.8 mm. wide, deltoid- to ovate-acuminate, the sinus acute to narrowly rounded; petals usually white, sometimes yellow or rose, rarely pale lilac, 7–11.5 mm. long, 2.5–4.8 mm. wide, obovate- to oblanceolate-spatulate or oblanceolate-cuneate, sometimes

with scattered glandular hairs 0.05 mm. long, attached to the staminal tube for 2–3 mm., the claw 1–3 mm. long.

Longistylous form. Stamens 4–5.8 mm. long, the filaments free for 1–2.5 mm., the anther 1.1–1.5 mm. long, 0.5–0.7 mm. wide, oblong, slightly emarginate at both ends, more so at the base; pistil 7.5–9.5 mm. long, the styles free for 3.4–4.5 mm., united for 1.5–3.5 mm., papillose for 1 mm. at the apex, the ovary ellipsoid to elliptic-ovoid, slightly pentagonal, the ovary and styles tomentulose, hairs stellate and forked, 0.1–0.5 mm. long, the stipe 0–0.5 mm. long.

Brevistylous form. Stamens 8–9.5 mm. long, the filaments free for 5–6.8 mm., the anther 1.1–1.7 mm. long, 0.6–0.7 mm. wide, shape the same as that above; pistil 5–5.7 mm. long, the styles free for 1.6–2.2 mm., united for 1.0–1.7 mm., papillose for 0.5–1.0 mm. at the apex, the ovary ellipsoid, occasionally of 6 carpels, hirsute or sericeous-tomentulose, the styles hirsute to their separation, hairs stellate, 0.2–0.8 mm. long, stipe none.

Fruit 5–7 mm. long of which 1–2 mm. is rostrum, 4.2–7.2 mm. wide, pentapterous, pyramidal, the sulci extending one-third of way to the center of the fruit, the angles of the wings near the middle of the fruit, short, acute to rounded, hirsute-tomentulose, hairs simple, forked, and stellate, 0.2–0.8 mm. long, stipe none; dehiscence loculicidal along the dorsal and ventral sutures; seeds 2–2.7 mm. long, 1.2–1.7 mm. wide, trigonal, obliquely obovate, brown to black, one per cell.

Flowering and fruiting specimens collected throughout the year.

Key to Varieties of *M. parvifolia*

1. Lamina subglabrous, hairs mostly simple, base usually cuneate.
41a. M. parvifolia var. **parvifolia**

1 Lamina hairier, sometimes lower surface tomentulose, hairs mostly stellate and forked, base more frequently rounded than in the typical variety.
41b. M. parvifolia var. **fasciculata**

41a. Melochia parvifolia H. B. K. var. **parvifolia**

? *Melochia parviflora* Loud. Hort. Brit. 269. 1830.
Melochia scordiifolia Turcz. Bull. Soc. Nat. Mosc. 31(1):207. 1858.
Melochia parvifolia α normalis O. Ktze. Rev. Gen. 3(2):25. 1898.
Melochia parvifolia β Esperanzae O. Ktze. Rev. Gen. 3(2):25. 1898.
Melochia parvifolia H.B.K. var. *genuina* Hassl. Repert. Sp. Nov. Fedde 8:120. 1910.
Melochia parvifolia H.B.K. var. *genuina* Hassl. f. *induta* Hassl. Repert. Sp. Nov. Fedde 8:120. 1910.
Melochia obovata Urb. Symb. Ant. 9:233. 1924.

The typical variety is sparsely hairy; the leaves are small, the lamina generally not exceeding 2.5 cm. in length and 1.3 cm. in width, and the base is usually cuneate.

TYPE LOCALITY: The type was collected by Humboldt in an arid region near Caracas, Venezuela.

DISTRIBUTION: Cuba and northern South America to Argentina, most commonly in savanna, also in campo and in cultivated and fallow land, in dry or moist places, in sandy or serpentine soil, and among granite rocks, at 0–1,400 meters elevation, mostly at lower elevations.

CUBA: ORIENTE: Santiago de Cuba, Siboney, *Bro. Clemente* 7005 (US). Santiago de Cuba, Vista Alegre, *Acuña & Morton* 3896 (US). Near Santiago de Cuba, *Ekman* 7694 (S, type of *Melochia obovata* Urb., also US neg. 5605), 8894 (S, isotype *M. obovata* Urb.). Siboney, *Morton* 3957 (US). Near El Cobre, *Bro. Clemente* 6285 (US); *Bro. León* 16773 (US).

BRITISH GUIANA: RUPUNUNI: Ireng River, 45 mi. N. of Lethem, *Irwin* 833 (US).

VENEZUELA: ?Cerro del Galipan, *Eggers* 13192 (L.) Lower Orinoco, Sacupana, *Rusby & Squires* 36 (MICH, R, S, US). Oronoco Delta, Cano del Uricoa-San Antonio, *Bond et al.* 134 (US). Las Trincheras, *Warming* 267 or 266 (US). Cumanacoa, *Mocquerys* 764 (US). "Venezuela, etc.," *Funck & Schlim* 564 (LE, and US neg. 5268, isotype of *Melochia scordiifolia* Turcz.). GUÁRICO: La Rubiera near Calabozo, *Grisol* 38 (US). Cordoncito, *Gines* 4121 (US). MIRANDA: Los Chorros, *Eggers* 13092 (US). Rio Chico, *Jahn* 1223 (US). Higuerote, *Gines* 4585 (US). FEDERAL DISTRICT: Caracas, *Humboldt*, F neg. 9807 of the type (US). Near Caracas, Middle Cotiza, *Pittier* 7213 (US). Around Caracas, San Lázara, *Pittier* 9746 (US). Around Caracas, *Pittier* 6171 (US). Sabana de Conejo Blanco, El Valle, *Fernández* 120 (US). ARAGUA: La Trinidad de Maracay, *Pittier* 5796 (US), 5820 (US). Maracay, *Vogl* 337 (S). Near colony of Tovar, *Fendler* 112 (GH). CARABOBO: Puerto Cabello, *Suringar* Mar. 1885 (L). ?CARABOBO: Puerto Cabello, *Kuntze* 1719 (US). COJEDÉS: Culebra Lagoon near S. Carlos, *Pittier* 11705 (US). APURE: Llanos del Alto-Apure, Hato Metapalo, *Jahn* 205 (US). Puerto Páez, *Valez* 2698 (US). Rio Meta, La Ochovera, *Cuatrecasas* 4183 (US). BOLÍVAR: Ciudad Bolívar, *Holt & Gehriger* 114 (US), 140 (US). Ciudad Bolívar and vicinity on the Orinoco, *L. H. & E. Z. Bailey* 1626 (US). Between Ciudad Bolívar and Rio Pao, *Killip* 37214 (US). Morichal Sta. Isabel, *Cardona* 699 in part (US). El Palmar, *L. Williams* 12869 (US).

COLOMBIA: ATLÁNTICO: Barranquilla and vicinity, *Fosberg* 21424 (US); *Bro. Elias* 109 (US), 178 (US), 274 (US), 995 (US), 1324 (US); *Dugand* 5437 (US), 5437 B (US), 5437 C (US). Usiacuri, *Dugand & Garcia Barriga* 2313 (US). Between Palmar de Varela and Ponedera on the banks of the Rio Magdalena, *Dugand & Garcia Barriga* 2541 (US). Between Sabanalarga and Campeche, *Dugand & Jaramillo* 2762 (US). Vicinity of Galapa and Baranoa, *Dugand & Jaramillo* 3269 (US). VICHADA: Puerto Carreño on the Rio Orinoco, *Cuatrecasas* 4067 (US).

BRAZIL: Western part, *Tamberlik* (W). RIO BRANCO: *Ule* 7971 (L, US). São Jorje, Rio Flexa, *Fróes* 23129 (US). SURUMU: Serra do Mel, *Ule* 8226 (L). AMAZONAS: S. Marcos, *Luetzelburg* 20509 in part (R), 20510 in part (R). GOIÁS: Porto Real to Santa Anna, *Burchell* 8856 (L), 9083 (L). MATO GROSSO; Cuiabá, ? *Riedel* 793 (K); *Malme* s.n. (S). Coxipó da Ponte, Cuiabá, *Hoehne* 3024 (R, US), 3025 (R). Porto Esperidião, *Hoehne* 775 (R). Corumbá, *Hoehne* 4839 (R), 4875 (R).

PARAGUAY: Rio Paraguay, ? Toncière, *Sandeman* 4873 (K). Alto-Paraguay, Chaco 21° S. lat., *Fiebrig* 1215 (S). Near Concepcion, *Hassler* 7399 (S). Road to "Yerbales" montium "Sierra de Maracayú," *Hassler* 4989 (S, W).

ARGENTINA: TUCUMÁN: MONTEROS: Kilometro 1220, *Herrera* 161 in part (S).

This species is close to *Melochia hermannioides* St.-Hil., but the latter is procumbent or decumbent and small, whereas *M. parvifolia* is generally erect and can be a tall shrub. The leaves of *M. hermannioides* are broader, rounder, and have larger teeth, and the flowers are rose, blue, purple or violet rather than generally white. The inflorescences of *M. hermannioides* are more frequently terminal and less frequently leaf-opposed. The species is also close to *Melochia morongii* Britt., but the latter has longer and narrower leaves which are hairier on the lower surface, and the apex is acutely pointed rather than rounded; the penduncles of *M. morongii* are longer. It is also related to *Melochia anomala* Griseb., but the leaves of the latter are generally larger, generally ovate rather than obovate, the serrations are larger, and the base rounded rather than often cuneate. The flowers are usually rose, blue, purple or violet rather than usually white.

41b. Melochia parvifolia H.B.K. var. **fasciculata** (Benth.) Hassl. Repert. Sp. Nov. Fedde 8:121 1910.

Melochia fasciculata Benth. *in* Hook. Journ. Bot. 4:127. 1841.
Melochia parvifolia H.B.K. f. *albiflora* Schum. & Hassl. Bull. Herb. Boiss. II, 4:70. 1903.
Melochia parvifolia H.B.K. var. *fasciculata* (Benth.) Hassl. f. *microphylla* Hassl. Repert. Sp. Nov. Fedde 8:121. 1910.
Melochia parvifolia H.B.K. var. *fasciculata* (Benth.) Hassl. f. *microphylla* Hassl. subf. *transiens* Hassl. Repert. Sp. Nov. Fedde 8:121. 1910.
Melochia parvifolia H.B.K. var. *fasciculata* (Benth.) Hassl. f. *typica* Hassl. Repert. Sp. Nov. Fedde 8:121. 1910.

This variety has hairier leaves, particularly on the lower surface, and the hairs are generally stellate and forked rather than simple. The lamina is often larger and the base is rounded rather than cuneate.

TYPE LOCALITY: The syntypes were collected by Schomburgk, no. 738, at Pirara, British Guiana, by Gardner, no. 2068 (?2060) in Piauí, Brazil, and by Blanchet, no. 2750, at Utinga, Belém, Pará, Brazil. Schomburgk no. 738 is cited below.

DISTRIBUTION: British Guiana, northern Brazil, and Paraguay in dry savannas, on rather humid cultivated areas, at about 200 meters elevation.

BRITISH GUIANA: Pirara, *Schomburgk* 738 (L, US, syntype of *Melochia fasciculata* Benth.), also F neg. 35379 ex P of *Schomburgk* 738 (US).

BRAZIL: AMAZONAS: Serra das Guaribas, *Luetzelburg* 21950 (R). Passarão, Rio Araricuera, *Luetzelburg* 20573 in part (R).

PARAGUAY: Colonia Risso near Rio Apa, *Malme* 1048 (S, US). Fuerte Olimpo, *Anisits* 2107 (S).

42. Melochia morongii Britt. Ann. New York Acad. Sci. 7:62. 1890.

Melochia Morongii Britt. var. *denudata* Fries, Svensk. Vet. Akad. Handl. 42(12):9. 1908.
Melochia parvifolia H.B.K. var. *Morongii* (Britt.) Hassl. Repert. Sp. Nov. Fedde 8:121. 1910.
Melochia parvifolia H.B.K. var. *Morongii* (Britt.) Hassl. f. *genuina* Hassl. Repert. Sp. Nov. Fedde 8:121. 1910.
Melochia parvifolia H.B.K. var. *Morongii* (Britt.) Hassl. f. *genuina* Hassl. subf. *denudata* (R. E. Fries) Hassl. Repert. Sp. Nov. Fedde 8:121. 1910.
Melochia parvifolia H.B.K. var. *Morongii* (Britt.) Hassl. f. *intermedia* Hassl. Repert. Sp. Nov. Fedde 8:121. 1910.
Melochia parvifolia H.B.K. var. *Morongii* (Britt.) Hassl. f. *tomentosa* Hassl. Repert. Sp. Nov. Fedde 8:122. 1910.

A branched, erect subshrub 0.3–0.6 meter high with 2–5 stems from the base, the root 0.8 cm. wide, 2–5 times as thick as the base of the stems, the young stems and petioles canescent, tomentose, hairs slender, stellate, 0.5–1.3 mm. long, internodes 2–6 cm. long; stipules 3.0–6.8 mm. long, 0.3–0.5 mm. wide, deltoid-acuminate, linear or lanceolate, mostly ciliate, hairs simple, 0.3–1.2 mm. long, a few forked and stellate, 0.2 mm. long; petiole 0.5–2.0 cm. long.

Lamina tomentulose, sometimes glabrescent, 2.0–7.5 cm. long, 0.8–3.0 cm. wide, ovate to lanceolate, the base rounded, the apex acute to rounded, the upper surface greenish or canescent, tomentulose, hairs simple, appressed, forked, and stellate, 0.1–1.0 mm. long, the lower surface canescent, tomentulose, hairs stellate, 0.3–0.7 mm. long, woolly to the touch, the margin irregularly crenate-serrate, serrations 1–5 mm. wide, 0.3–1.2 mm. high, 5–10 pairs of primary veins, 1 or 2 are basal.

Inflorescences leaf-opposed, 2.5–7.0 cm. long, sometimes also axillary, 1–1.5 cm. long, at 2–4 nodes, and terminal, extending 3–3.6 cm. beyond the first leaf, in subcapitate umbels, 5–12 flowers per umbel, the peduncle usually fairly long, 0.7–4.0 cm. long, 0.6–1.4 mm. wide, sometimes with a branch 1 cm. long, the pedicel 2–5 mm. long; bracts 1.5–5.0 mm. long, 0.1–0.3 mm. wide, linear, ciliate and tomentulose, hairs simple, forked, and stellate, 0.2–1.1 mm. long.

Calyx 6.7–10.2 mm. long, 4–5 mm. wide, densely tomentulose, hairs stellate and forked, 0.1–1.0 mm. long, the teeth 4.5–7.8 mm. long, 1.3–1.7 mm. wide, lanceolate- to deltoid-acuminate, the sinus acute to slightly rounded; petals blue, purple, lilac, or dirty white, 9.5–11.5 mm. long, 2.0–3.8 mm. wide, obovate-oblanceolate or obovate-oblong, attached to the stamens for 1–3.3 mm., the claw 1–3 mm. long, sometimes glandular hairs 0.05 mm. long scattered over both surfaces.

Longistylous form. Stamens 5.5 mm. long, the filaments free for 2.0–2.3 mm., the anther 1.3–1.4 mm. long, 0.7 mm. wide, oblong, slightly emarginate at both ends; pistil 10.5 mm. long, the styles free for 4.5–6.5 mm., united for 1.5–4.0 mm., filiform, papillose for 1.5 mm. at the apex, the ovary and styles tomentulose, hairs stellate, 0.2–0.5 mm. long, the ovary ovoid, stipe none.

Brevistylous form. Stamens 8.1–10.5 mm. long, the filaments free for 6.0–7.5 mm., the anther 1.3–1.8 mm. long, 0.5–0.8 mm. wide, shape the same as that above, staminodes sometimes present, 0.1–0.2 mm. long; pistil 5.0–6.5 mm. long, the styles free for 1.5–2.5 mm., united for 1–2 mm., filiform, papillose for 0.7–1.0 mm. at the apex, the ovary elliptic-ovoid, united parts of the styles and upper part of the ovary hirsute-tomentulose, hairs stellate and forked, 0.2–1.0 mm. long.

Fruit 6–7 mm. long, of which the rostrum is 1.5–2.0 mm. long, 4.0–5.8 mm. wide, pentapterous, pyramidal, the wings short, points near the middle of the fruit, angle acute to rounded, the sulci extending a fourth to half way to the center of the fruit, tomentulose, hairs stellate, 0.1–0.6 mm. long, the stipe of glandular tissue 0–0.3 mm. long; dehiscence loculicidal all along the dorsal suture; seeds 2.4–2.6 mm. long, 1.5–1.7 mm. wide, brown, one per cell.

Flowering and fruiting specimens collected from October to February.

TYPE LOCALITY: The type was collected by Morong, no. 201a, at Asunción, Paraguay, and is cited below.

DISTRIBUTION: Southwestern Brazil, Paraguay, and Misiones, Argentina, in grassy fields, in a valley, on cultivated land, and on calcareous campo, at 220–225 meters elevation.

BRAZIL: MINAS GERAIS: Ituiutaba, *Macedo* 1034 (US). GOIÁS: Jataí, Balsam, *Macedo* 1504 (US).

PARAGUAY: *Anisits* 2731 (S). Est. Santa Maria, *Anisits* 2529 (S, type of *Melochia morongii* Britt. var. *denudata* R. E. Fries, also U.S. neg. 5613). Est. Tagatiya, *Anisits* 2640 (S). Asunción, *Morong* 201a (NY, type; US, isotype). Along road between Caacupé and Tobaty, *Archer & Rojas* 4864 (US). Rio Apa, *Hassler* 7744 (S, W). Centurion, between Rio Apa and Rio Aquidaban, *Fiebrig* 4620 (L). CANTERA: Colonia Alborada, *Montes* 3254 (US). GRAN CHACO: On the western bank of the River Paraguay, *Hassler* 2406 (K), 2406a (K).

ARGENTINA: MISIONES: CANDELARIA: Loreto, *Montes* 24B (US); *Ekman* 178 (US).

Fries (15) made the variety *denudata* on the basis of the glabrescent nature of the leaves of some specimens. There is considerable variation in the vestiture of the leaves, but I consider the transition from one type to another to be too gradual to warrant making a variety based on vestiture alone. Hassler (23) considered *M. morongii* to be a variety of *M. parvifolia* H.B.K., and he described three forms in the

variety. The leaves of *M. morongii* are generally ovate to lanceolate, those of *M. parvifolia* are usually obovate to elliptic. The leaves are usually larger and usually hairier than those of *M. parvifolia*. The peduncle is usually longer than that of *M. parvifolia*. *Melochia parvifolia* is a taller plant and its flowers are usually white rather than usually colored.

The species is also related to *M. anomala* Griseb., but the inflorescences and peduncle are shorter in the latter species, and the serrations of the leaves are usually larger.

43. Melochia anomala Griseb. Abh. Wiss. Goett. 19:93. 1874. PLATE 7

A more or less erect shrub 0.5–1 meter high with several (4) stems from the base, the root thickened, 0.5–1.0 cm. wide, twice the diameter of the stem, the young stems and petioles usually lightly tomentose-hirsute, somewhat canescent, hairs simple, forked, and stellate, 0.3–1.4 mm. long, internodes 1–5.5 cm. long; stipules 3.5–6.0 mm. long, 0.2–0.9 mm. wide, deltoid-acuminate, lanceolate, or nearly linear, ciliate, also a few simple hairs, rarely also forked on the abaxial surface, 0.3–1.2 mm. long; petiole 0.2–2.5 cm. long.

Lamina 1–6 cm. long, 0.8–4.0 cm. wide, ovate, ovate-lanceolate, lanceolate, or oblong, the base rounded, the apex rounded to acute, the upper surface green, covered with appressed simple hairs, rarely also forked and stellate, 0.2–1.3 mm. long, the lower surface lightly tomentose, slightly canescent, hairs usually simple, forked, and stellate, 0.3–1.2 mm. long, the margin irregularly crenate-serrate almost to the base, serrations 1–3.8 mm. wide, 0.4–2.5 mm. high, 6–7 (–10) pairs of primary veins, 2 are basal.

Inflorescences leaf-opposed at 3–6 upper nodes, in subcapitate umbels 1–1.3 (–3.0) cm. long, 3–7 (–12) flowers per umbel, the peduncle 0–0.5 (–2.3) cm. long, the pedicel 1–2 mm. long; bracts 3–5.5 mm. long, 0.2–0.5 mm. wide, linear to lanceolate, mostly ciliate, few hairs on the abaxial surface, hairs simple, 0.2–1.3 mm. long.

Calyx 7–7.5 mm. long, 5.6–6.0 mm. wide, tomentose-canescent, also ciliate, hairs simple, forked, and stellate, 0.1–1.3 mm. long, the teeth 5–6 mm. long, 1.2–1.8 mm. wide, deltoid- to lanceolate-acuminate, the sinus narrowly rounded; petals violet, purple, rose, blue, rarely whitish, 9.8–10.5 mm. long, (1.7–) 3.5–3.9 mm. wide, usually obovate, with scattered glandular hairs 0.05 mm. long, attached to the staminal tube for 2–3 mm., the claw 1–2.5 mm. long.

Longistylous form. Stamens 5.4–5.7 mm. long, the filaments free for 1.6–2.5 mm., the anther 1.3–1.6 mm. long, 0.6–1.0 mm. wide, oblong, slightly emarginate at both ends; pistil 7.8 mm. long, the styles filiform, free for 3.4–3.7 mm., united for 2 mm., papillose for 0.8–1.0 mm., the ovary ovoid, mostly upper part with forked and

stellate hairs 0.3–1.0 mm. long, and stellate hairs 0.2 mm. long nearly to the tips of the styles.

Brevistylous form not seen.

Fruit (5–) 6.5–8.0 mm. long, of which the rostrum is 2.0–2.5 mm., (5.5–) 6.2–7.0 (–9.0) mm. wide, pentapterous, pyramidal, the angle of wing acute, about the middle of the fruit, the sulci extending one-third the way to the center of the fruit, tomentulose, hairs stellate, 0.1–0.5 mm. long, a few forked, up to 0.7 mm. long, stipe none; dehiscence loculicidal along the dorsal suture; seeds (not ripe) 2.5 mm. long, 1.5 mm. wide, obovate, trigonal, brownish, one per cell.

Flowering specimens collected from October to April; fruiting ones, from October to May.

TYPE LOCALITY: On hills exposed to the sun near Malagueño, Córdoba, Argentina. Type collected by Lorentz, no. 503, cited below.

DISTRIBUTION: Bolivia and Argentina on slopes of hills in red soil, campo, uncultivated, dry, hard land, at 100–1,200 meters elevation.

BOLIVIA: SANTA CRUZ: *Weddell* 3588 (P). Cabezas (Cordillera), *Peredo* 39 (UC), 260 (UC). A. IBAÑEZ: La Guardia, *Krapovickas* 9038 (LIL). TARIJA: *Fries* 1135 (S).

ARGENTINA: SALTA: ANTILLAS: Cerro Negro, *Venturi* 10292 (A, S, US). ORÁN: Tartagal, *Schreiter* 3893 (S). Abra Grande, *Venturi* 5519 (GH, S, US). La Cantera, *Pierotti* 205 (UC). La Calera, *Pierotti* 197 (UC). At foot of hill E. of Salta, *Bartlett* 19722 (US). "Monte" at Experiment Station, Coronel Moldes, *Bartlett* 19668 (US). Capital, San Lorenzo, *Venturi* 5085 (A, US). Joaquin V. Gonzáles, *Aguilar* 257 (UC). TUCUMÁN: BURROYACO: El Puestito, *Venturi* 7529 (S, US). El Timbó, *Venturi* 2430 (US). RIO CHICO: La Cocha, *Bailetti* 9 (S). CAPITAL: Rio Sali, *Venturi* 2756 (A, US). ?Mataderos, *Venturi* 2190 in part (US). TRANCAS: Tapia, *Venturi* 2360 (A, US). Road to S. Pedro de Colalao, *Venturi* 4219 (US). CRUZ ALTA: Campo Alegre, *Venturi* 2012 (US). Las Cajas, *Venturi* 2108 (US). SANTIAGO DEL ESTERO: C. PELLEGRINI: Carro del Remate, *Venturi* 5972 (GH, US). CHACO: Border of Rio Las Garzas, *E. R. Wagner* s.n. (P). NAPALPÍ: Pampa del Infierno, *Buratovich* 525 (W). CÓRDOBA: *Kuntze* Dec. 1891 (NY). F neg. 9596 ex. B of *Lorentz* 110 (US). Malegueño, foothills of Córdoba, *Lorentz* 503 (GOET, type, also US neg. 5239). Pueblo Güemes, *Ruiz de Huidobri* 413 (UC). PUNILLA: San Roque, *Hunziker* dupl. 5997 (S).

This species is closely related to *M. hermannioides* St.-Hil., but *M. anomala* has larger leaves and usually shorter peduncles. The entire plant is hairier, particularly the leaf and calyx. It is also related to *M. parvifolia* H.B.K., but it has larger, hairier leaves with larger serrations.

44. Melochia werdermannii A. Goldberg, sp. nov. PLATE 8

Suffrutex, utrinque valde tomentosus molle incanus, pilis stellatis, 0.3–1.0 mm. longis praeditus; petiolis 1–1.7 cm. longis; laminis foliorum 4.5–7.0 cm. longis, 2.2–4.9 cm. latis, ovatis vel aliquatenis rotundatis; inflorescentiis oppositifoliis, cymoso-umbellatis, umbellis 5–15 floris, pedunculis brevis et crassis, 0.2–0.8 cm. longis, 1.2–1.5

mm. latis, pedicellis brevis, 1.5–2.5 mm. longis; calycibus 7–9.2 mm. longis; fructibus perangustatis, 6–7 mm. longis, 3.8–4.8 mm. latis, pentapteris, pyramidatis, angustatis ad basin, alis perangustatis, acuminibus lateralibus rotundatis vel subacutis, sessilibus; dorsaliter plene loculicide vix septicide dehiscentibus.

An erect, usually branched suffrutex, the young stems and petioles densely tomentose, canescent, hairs stellate, 0.5–1.0 mm. long, internodes 2–6 cm. long; stipules 4–6.5 mm. long, 0.5–0.8 mm. wide, lanceolate, densely tomentose, hairs stellate, 0.2–0.5 mm. long; petiole 1–1.7 cm. long.

Lamina 4.5–7.0 cm. long, 2.2–4.9 cm. wide, lanceolate-ovate to ovate, sometimes also suboblong, the base rounded, the apex acute to somewhat rounded, both surfaces densely tomentose, canescent, hairs stellate, 0.3–0.5 mm. long, velvety to the touch, the margin irregularly crenate-serrate, serrations 1–6 mm. wide, 0.3–1.6 mm. high, 10–12 pairs of primary veins, 2 are basal.

Inflorescences 1–2 cm. long, leaf-opposed, at 5–9 nodes, umbellate, 5–15 flowers per umbel, the peduncle short and relatively thick, 0.2–0.8 cm. long, 1.2–1.5 mm. wide, the pedicel 1.5–2.5 mm. long; bracts 2–5.3 mm. long, 0.2–0.6 mm. wide, linear to lanceolate, tomentose, hairs stellate, few forked and simple, 0.2–1.8 mm. long.

Calyx 7–9.2 mm. long, 4.3–5.5 mm. wide, densely tomentose, canescent, hairs stellate, 0.2–0.7 mm. long, the teeth 4.7–5.7 mm. long, 1.7–2.3 mm. wide, deltoid- to ovate-acuminate, or sublanceolate, the midrib often prominent, the sinus acute to narrowly rounded; petals 7.5–10.8 mm. long, 1.5–3.4 mm. wide, obovate-oblanceolate, attached to the staminal tube for 2.5–3.0 mm., the claw 1.5–3.0 mm. long, with scattered glandular hairs 0.05 mm. long, faint indication of purple or rose in the dried condition.

Longistylous form. Stamens 4.7–5.8 mm. long, the filaments free for 1.7 mm., the anther 1.5 mm. long, 0.8 mm. wide, oblong, slightly emarginate at both ends; pistil 7.2 mm. long, the styles free for 3.2 mm.

Brevistylous form. Stamens 7–10 mm. long, the filaments free for 4.0–6.5 mm., the anther 1.6–1.8 mm. long, 0.6–0.9 mm. wide, shape same as that above; pistil 5.2–5.7 mm. long, the styles filiform, free for 1.5–1.8 mm., united for 0.5–1.5 mm., stigmatic for 0.3–0.7 mm., the ovary ovoid, considerably narrowed at the base, tomentulose, hairs stellate, 0.2–0.3 mm. long.

Fruit narrow, 6–7 mm. long, 3.8–4.8 mm. wide, narrowed toward the base, the rostrum 1.2–2.0 mm. long, pentapterous, pyramidal, the wings very narrow, outer angle of the wing slightly below the middle of the fruit, rounded to subacute, the sulci between the carpels

extending a fifth to a third of way to the center of the fruit, tomentulose, hairs stellate, 0.2–0.3 mm. long, stipe none; dehiscence loculicidal all along the dorsal suture, sometimes tardily so, very slightly septicidal; seeds 2.4–2.9 mm. long, 1.4–1.6 mm. wide, obovate, trigonal, brown, 1 per cell.

Flowering and fruiting specimens collected in February and October, few fruits present in the latter month.

TYPE LOCALITY: Missiones Guarayos-Santa Cruz de la Sierra, Santa Cruz, Bolivia. The type was collected by Werdermann, no. 2606, and is cited below.

DISTRIBUTION: Santa Cruz, Bolivia, at 250–300 meters elevation.

BOLIVIA: SANTA CRUZ: Missiones Guarayos-Santa Cruz de la Sierra, *Werdermann* 2606 (S, type, also US neg. 5607). CHIQUITOS: Roboré, *Krapovickas* 9190 (LIL).

This species differs from the other densely stellate-tomentulose, canescent species of this section in having the following combination of characters: Very narrow fruits, short, thick peduncles, and a relatively large lamina, velvety to the touch. It is most closely related to *M. anomala*.

45. Melochia illicioides Schum. *in* Mart. Fl. Bras. 12(3):31. 1886.
Melochia decandra "Willd." ex Schum. *in* Mart. Fl. Bras. 12(3):31. 1886, in synonymy.

A simple or branched erect suffrutex up to 1 meter high, the young stems tomentulose-canescent, hairs stellate, 0.1–0.2 mm. long, internodes 1–8 cm. long; stipules caducous, 1.7 mm. long, 1 mm. wide, deltoid-acute, tomentulose, hairs stellate, 0.1 mm. long; petiole 0.4–3.3 cm. long.

Lamina 2–5.2 cm. long, 1.2–3.6 cm. wide, lanceolate to lanceolate-ovate, the base subcordate, the apex acute, the upper surface greenish-canescent, tomentulose, hairs stellate, 0.1 mm. long, the lower surface canescent, tomentulose, hairs stellate, 0.1–0.2 mm. long, both surfaces velvety to the touch, the margin irregularly crenate-serrate, serrations 1.2–6.0 mm. wide, 0.5–1.6 mm. high, 8 pairs of primary veins, 2 are basal.

Inflorescences at the upper 3–7 nodes, apparently axillary and leaf-opposed at the same node, or one cluster at a node, 1.5–3.0 cm. long, apparently sometimes also terminal, extending 1.7 cm. beyond the first leaf, umbellate, 3–6 flowers per umbel, the peduncle 0.4–1.5 (–2.5, Schum.) cm. long, sometimes with a primary branch 0.5–1.1 cm. long and a secondary branch 0.5 cm. long, the pedicel 1.7–4.0 mm. long; bracts 1–1.7 mm. long, 0.2–0.5 mm. wide, lanceolate to nearly linear, tomentulose, hairs stellate, 0.1 mm. long.

Calyx 5.2 mm. long, 4.2 mm. wide, tomentulose-canescent, hairs stellate, 0.1–0.2 mm. long, also a few glandular granules and glandular hairs 0.1–0.2 mm. long, the teeth 3–3.5 mm. high, 1.5 mm. wide, deltoid-acuminate, the sinus acute to slightly rounded; petals white, 9–9.7 mm. long, 2 mm. wide, oblanceolate, the claw 3–4 mm. long, united to the staminal tube for 2.7 mm.

Longistylous form. Stamens 5.5 mm. long, the filaments free for 1.5 mm., the anther 1.1 mm. long, 0.7 mm. wide, oblong, emarginate at both ends; pistil 9 mm. long, the styles filiform, free for 5.5 mm., united for 1 mm., papillose for 0.8 mm. at the apex, the ovary pentagonal-ovoid, tomentulose, hairs stellate, 0.1–0.2 mm. long, the styles with scattered hairs up to the stigmas.

Brevistylous form (according to Schumann). Stamens 8 mm. long, the filaments filiform, free for 6 mm., the anther 1.5 mm. long, deeply divided, divergent above; pistil 4 mm. long, the ovary setose at the apex, the styles flat and free (in one specimen 6), the apex clavate, slightly thickened, glabrous.

Fruit relatively large, 1–1.2 cm. long, 1.9–2.2 cm. wide, chartaceous, pentapterous, pyramidal, truncate at the apex or with a short rostrum 1 mm. long, the outer angle of wings basal, rounded and mucronate for 0.2 mm., or acute, the sulci between the carpels extending half way to the center of the fruit, stipe none, but the base of the capsule stipelike for 0.5 mm., sometimes 6–7 carpels; dehiscence loculicidal along the dorsal and ventral sutures; seeds (Schumann) 2.5 mm. long, compressed, black, glabrous, chalaza large, cinereous-fuscous.

TYPE LOCALITY: Bahia State, Brazil, near Barra da Vareda. Type collected by Prinz zu Wied-Neuwied, number 2.

DISTRIBUTION: Bahia, Brazil, and Honda, Colombia (Schumann), in forest and along roads.

BRAZIL: F neg. 9604 ex B (US). BAHIA: Maritiba, *Blanchet* 3472 (NY).

This species can be distinguished from other species by its relatively large capsules that are chartaceous rather than somewhat indurate and truncate or very shortly rostrate rather than long rostrate. It is perhaps most closely related to *Melochia betonicifolia* St.-Hil.

The collection of the specimen photographed as F 9604 ex B is attributed to Poeppig, no. 2519, but Schumann (47) cited Poeppig 2519 as *M. littoralis* (Poepp. & Endl.) Schum. The photograph fits the description of *M. illicioides* Schum., and the specimen was identified as such by Schumann. Since there is a number 2 pasted on the specimen sheet, the specimen may have been collected by Prinz zu Wied-Neuwied, number 2, which is the only Brazilian collection of this species mentioned by Schumann (47).

46. Melochia betonicifolia St.-Hil. Fl. Bras. Mer. 1:165. 1825.
Melochia nepetoides St.-Hil. Fl. Bras. Mer. 1:165. 1825.
Melochia cordiformis St.-Hil. Fl. Bras. Mer. 1:166. 1825.

A branched, erect suffrutex to frutex, 0.45–4.0 meters high, the young stems and petioles tan-canescent, tomentulose, hairs stellate, 0.1–1.0 mm. long, internodes 0.3–5.0 cm. long; stipules 1.7–8.0 mm. long, 0.4–3.7 mm. wide, deltoid-acuminate or deltoid-acute or lanceolate, tomentulose on the abaxial surface, also ciliate, hairs simple, forked, and stellate, 0.1–1.2 mm. long; petiole 0.5–4.4 cm. long.

Lamina 2.5–8.0 cm. long, 1.2–5.8 cm. wide, ovate to lanceolate, the base rounded to cordate, the apex acute, the upper surface green, hirsute-tomentulose, hairs stellate, forked, and simple, 0.1–0.5 (–0.8) mm. long, the lower surface greenish or slightly to considerably canescent, tomentulose, hairs stellate, 0.1–0.6 mm. long, velvety or rough to the touch, the margin irregularly crenate-serrate, serrations 1.1–7.0 mm. wide, 0.5–2.6 mm. high, (5–) 7–10 pairs of primary veins, 2 (1–3) are basal.

Inflorescences 1.3–4.7 cm. long, usually axillary at the upper 2–5 nodes, rarely also terminal and leaf-opposed, sometimes on short axillary branches, the clusters in subcapitate umbels of 5–20 flowers, the peduncles (0.2–) 0.8–2.9 cm. long, 1–1.2 mm. wide, rarely with a branch 0.2 cm. long, the pedicel 1–3.7 mm. long; bracts 1–4.5 mm. long, 0.2–1.2 mm. wide, deltoid-acuminate or deltoid-acute to lanceolate and linear, hirsute-tomentulose and ciliate, hairs simple, forked, and stellate, 0.1–0.8 mm. long.

Calyx 6–8.3 mm. long, 4.5–6.0 mm. wide, canescent, densely tomentulose, hairs stellate and sometimes also forked, 0.1–0.3 (–1.0) mm. long, the teeth 3.3–5.3 mm. long, 1.5–2.4 mm. wide, deltoid to ovate, acuminate or acute, the sinus acute to rounded; petals white, yellow or purple, 7.5–12.5 mm. long, 2–4.5 mm. wide, oblanceolate- or obovate-cuneate, attached to the staminal tube for 1–4.5 mm., the claw 2–3 mm. long.

Longistylous form. Stamens 5.5–7.1 mm. long, the filaments free for 0.7–1.5 mm., the anther 1.1–1.4 mm. long, 0.5–0.7 mm. wide, oblong, slightly emarginate at both ends; pistil 8.4–10.4 mm. long, the styles filiform, free for 4.3–6.7 mm., united for 1–2 mm., papillose for 0.7–1 mm. at the apex, the ovary ellipsoid-ovoid, the styles and ovary hirsute-tomentulose, hairs stellate, forked and simple, 0.1–0.6 mm. long, sometimes 7 carpels present, the stipe 0.1 mm. long.

Brevistylous form. Stamens 6.5–10.2 mm. long, the filaments free for 2.5–6.0 mm., the anther 0.8–1.4 mm. long, 0.6–0.8 mm. wide; pistil 5–5.2 mm. long, the styles free for 2–4 mm., united for 1–2.8 mm., slightly clavate and stigmatic for 0.5–0.7 mm., the styles and ovary tomentulose, hairs stellate, 0.2–1.0 mm. long.

Fruit sometimes with 8 carpels, 6.7–8.5 mm. long, 2.5 mm. being rostrum, 11.5–17 mm. wide, pyramidal, pentapterous, the points of wings acuminate, tomentulose, hairs stellate, 0.2–1.0 mm. long, the capsule narrowed at the base for 1 mm., the stipe 0.5 mm. long; dehiscence loculicidal along the dorsal and ventral sutures; seeds 2.5–2.7 mm. long, 1.6–1.8 mm. wide, brown.

Flowering specimens collected from December to February, April to June, and in August and September; fruiting ones, in February, April, August, and September.

TYPE LOCALITY: The type was collected by St.-Hilaire near the praediolum Bom Jardin, not far from the praesidio called S. Miguel de Jiquitinhonha in Minas Gerais, Brazil, commonly in caatinga woods where the leaves are shed every year. The isotype is cited below.

DISTRIBUTION: Northern and eastern Brazil in caatinga woods in which the leaves are shed during the hot and dry season, at low elevations (50 meters).

BRAZIL: CEARÁ: Four km. S. of Mecejana, *Cutler* 8393 (US). Fortaleza, Aldeota, *Ducke* 2377 (US). PERNAMBUCO: Paquaretinga, *Pickel* 1504 (US). BAHIA: Maracás, *Ule* 6967 (K, L). S. Thome, *Blanchet* 3791 (P). ?BAHIA: Coraçao, *Blanchet* 3306 (NY, P). MINAS GERAIS: S. Miguel da Jequitinhonha, *St.-Hilaire* cat. B_1 1561 (P, isotype), also F neg. 35377 ex P (US). Near S. Domingos, St.-Hilaire cat. B_1 1579 (P, type of *Melochia cordiformis* St.-Hil., also F neg. 35378 ex P [US]). Rivulet Sucuriù, *St.-Hilaire* 1405 (P, isotype of *Melochia nepetoides* St.-Hil., also F neg. 35384 ex P (US). Arassuahy near Rio Manso, *Glaziou* 13557 (P), in part (R). RIO DE JANEIRO: Environs of Rio de Janeiro, *Glaziou* 13557 (K). Serra da Estrella, *Glaziou* 12459 (R).

This species is similar to *M. tomentosa* L., but generally more robust; the inflorescences generally contain more flowers, often white or yellow; the pedicels are usually shorter. It is also related to *M. caracasana* Jacq.; the inflorescence is usually leaf-opposed in *M. caracasana*, but usually axillary in *M. betonicifolia*. The capsules are generally wider in *M. betonicifolia* than in *M. caracasana*.

M. betonicifolia, *M. nepetoides*, and *M. cordiformis* were published at the same time. In combining them, in accordance with the International Code of Botanical Nomenclature (33), I select *M. betonicifolia* as the correct name.

47. Melochia caracasana Jacq. Coll. 2:369. 1788.
Melochia macrophylla H.B.K. Nov. Gen. & Sp. 5:324. 1823.
Mougeotia caracasana (Jacq.) H.B.K. Nov. Gen. & Sp. 5:329. 1823.
Riedleia Caracasana (Jacq.) DC. Prodr. 1:492. 1824.
Visenia caracasana (Jacq.) Spreng. Syst. 3:30. 1826.

An erect, branched shrub, sometimes herb, 0.45–5.0 meters high, the young stems sordid canescent, densely tomentose, hairs stellate, 0.3–1.0 mm. long, internodes 1–9 cm. long; stipules 2–7 mm. long,

1.2–2.0 mm. wide, deltoid-acute to deltoid-acuminate, tomentose and ciliate, hairs simple and forked, 0.2–1.0 mm. long; petiole 0.5–5.1 cm. long.

Lamina 1.4–12.7 cm. long, 0.8–7.7 cm. wide, lanceolate-ovate to ovate, the base rounded to cordate, the apex usually acute, the upper surface green, sparsely to densely puberulous, hairs stellate, forked and simple, 0.4 (0.2–0.9) mm. long, the lower surface yellowish-tan-canescent, tomentose, hairs stellate, 0.3–0.8 mm. long, both surfaces woolly to the touch, the margin irregularly crenate to crenate-serrate, crenations or serrations 2–5 mm. wide, 0.7–2.0 mm. high, 5–10 pairs of primary veins, 2 are basal.

Inflorescences 1–3 cm. long, leaf-opposed, axillary, or both, at the upper 2–6 nodes, apparently sometimes also terminal, the clusters in rather dense subcapitate umbels of 3–20 flowers, the flowers fragrant, the peduncle thick, 0.4–2 cm. long, 0.8–1.4 mm. wide, sometimes with a branch 0.3–0.5 cm. long, the pedicel 1–4 mm. long; bracts 1.8–6.0 mm. long, 0.2–1.0 mm. wide, deltoid-acute to deltoid-acuminate, or linear, tomentose.

Calyx 5–8 mm. long, 3.5–6.0 mm. wide, sordid canescent and tomentulose, hairs stellate, 0.3 (–2.0) mm. long, the teeth 2.5–6.0 mm. long, 0.8–2.0 mm. wide, deltoid-acute to deltoid-acuminate, sometimes with rounded sides, the sinus usually acute; petals white to yellow and brownish, 6–10 mm. long, 1.5–2.6 mm. wide, oblanceolate to obovate, spatulate, attached to the staminal tube for 1.5–1.8 mm., the claw 1 mm. long.

Longistylous form. Stamens 5.0–6.5 mm. long, the filaments free for 1–3 mm., the anther 1.4–1.7 mm. long, 0.5–1.0 mm. wide, oblong, emarginate at both ends; pistil 7.2–10 mm. long, the styles filiform, free for 4.5–6.0 mm., united for 1.6 mm., papillose and slightly clavate for 0.5–1.0 mm. at the apex, the ovary ovoid to ellipsoid, slightly pentagonal, hirsute at the apex, hairs stellate, forked and simple, 0.2–0.7 mm. long, the stipe 0–0.8 mm. long.

Brevistylous form. Stamens 7–8.5 mm. long, the filaments free for 4–5.5 mm., the anther 0.8–1.6 mm. long, 0.4–0.7 mm. wide, ellipsoid, ovoid, or oblong and emarginate at both ends; pistil 4–6.5 mm. long, the styles 1.5–2 mm. long, free to the ovary.

Fruit 7–10 mm. long, 2 mm. is rostrum, 6–11 mm. wide, pyramidal, pentapterous, the points of wings usually basal, usually recurved and acute to acuminate, rarely blunt, usually canescent, densely pubescent, hairs stellate, up to 0.5 mm. long, the stipe 0–1 mm. long; dehiscence loculicidal along the dorsal suture; seeds 2.2–2.7 mm. long, 1.1–1.5 mm. wide, trigonous, brown, sometimes striate.

Flowering and fruiting specimens collected in May, June, and August to December.

TYPE LOCALITY: The type was collected by Jacquin near Caracas, Venezuela, and is cited below.

DISTRIBUTION: Northern Venezuela, Colombia and Brazil, in thickets, on open, dry, rocky hillside, in ravines, or in savannas, at 0–1,700 meters elevation.

VENEZUELA: SUCRE: F neg. 35383 ex P of type of *Melochia macrophylla* H.B.K. (US). MIRANDA: Petare and vicinity, near Caracas, *Pittier* 7146 (US). FEDERAL DISTRICT: Caracas, *Jacquin* (W, type); *van Landsberge* 253 (S); *Pittier* 6149 (US). El Valle, *Fernández* 154 (US). On road to La Guaira from Caracas, between Catia and Las Trincheras, *E. Pittier* 12 (US). Lower Cotiza, *Pittier* 7178 (US). Turmerito, Ingomar, *Killip* 37728 (US). El Paraiso, Caracas, *Lasser* 744 (US). Between Caracas and La Guaira, *Mr. & Mrs. J. N. Rose* 21820 (US). On the old road from Caracas to La Guaira, *Pittier* 9545 (US). La Guaira, *André* 109 (NY). ?FEDERAL DISTRICT: Valle, *van Landsberge* NOV. 1847 (S). El Valle and Laguna de Espino, *Eggers* 13130 (L, US). ARAGUA: Maracay, *Vogel* 340 (S). Colonia Tovar, *Fendler* 109 (P, US). CARABOBO: Hacienda Taborda, near El Palito, on the road from Valencia to Puerto Cabello, *Pittier* 7666 (US). Puerto Cabello, Valle Seco, *Engstedt* 3 (S). El Palito, Valencia, *Warming* 264 (US). LARA: Near Barquisimeto, *Saer* 26 (US). MÉRIDA: *Mocquerys* 1234 (US).

COLOMBIA: MAGDALENA: Santa Marta, *Dawe* 500 (US). SANTANDER: Río Suratá valley, near Bucaramanga, *Killip & Smith* 16226 (US).

BRAZIL: CEARÁ: *Allemão & de Cysneiros* 134 (R, US).

This species is similar to *M. tomentosa* L., but generally larger and more robust; the inflorescences generally contain more flowers, white or yellow rather than purple; the peduncles are thicker; the pedicels are usually shorter; the leaves have longer hairs. It is also similar to *M. betonicifolia* St.-Hil., but the inflorescence is most commonly axillary in *M. betonicifolia* and usually leaf-opposed in *M. caracasana*. The leaves of *M. caracasana* are usually hairier than those of *M. betonicifolia* and the hairs are yellowish rather than white.

It is illustrated by Jacquin (32).

48. Melochia lanata St.-Hil. Fl. Bras. Mer. 1:167. 1825.

Melochia lanata St.-Hil. var. *inclusa* St.-Hil. Fl. Bras. Mer. 1:167. 1825.

An erect, branched suffrutex, at least 0.4 meter high, the young stems and petioles densely lanate, canescent, hairs stellate and apparently forked and simple, 0.2–1.6 mm. long, internodes 2–7 cm. long; stipules 4.1–7.0 mm. long, 0.2–0.5 mm. wide, lanceolate to sub-linear, mostly ciliate, some hairs on the abaxial surface, most simple, some forked, 0.4–2.0 mm. long; petiole 0.5–1.5 cm. long.

Lamina 2–5.5 cm. long, 1–3.4 cm. wide, ovate, ovate-lanceolate, lanceolate, oval or elliptic-oblong, the base rounded, the apex rounded or acute, the upper surface sericeous-tomentose, lanate, hairs yellowish-tan-canescent, simple, appressed, 0.5–2.0 mm. long, the lower surface densely lanate, yellowish- to tan-canescent, hairs stellate, forked, and simple, 0.7–1.6 mm. long, the margin irregularly and mostly shallowly

crenate-serrate, serrations 0.8–3.9 mm. wide, 0.3–1.3 mm. high, 7–9 pairs of primary veins, 2 are basal.

Inflorescences 2–5 cm. long, leaf-opposed, 90° from the leaf, or axillary, 3–15 flowers in dense subcapitate, umbellate clusters at 3–6 upper leaf nodes, 1 or 2 clusters per peduncle, the peduncle 0–3 cm. long, 1.2 mm. wide, the pedicel 2–4 mm. long; bracts 2.5–6.5 mm. long, 0.2–0.3 mm. wide, sublinear to linear, lanate-tomentose and ciliate, hairs mostly simple, few forked, 0.3–1.8 mm. long.

Calyx 6.8–9.2 mm. long, 4.7–5.2 mm. wide, lanate-tomentose on the outside, hairs stellate, forked and simple, 0.2–1.5 mm. long, the teeth 3.8–5.8 mm. long, 2–2.2 mm. wide, ovate- to deltoid-acuminate, the sinus acute; petals 8.6–14 mm. long, 2.2–2.5 mm. wide, oblanceolate, with scattered glandular hairs 0.05 mm. long, attached to the staminal tube for 3.5–3.7 mm., the claw 1.5–2.5 mm. long.

Longistylous form not seen.

Brevistylous form. Stamens 7.7–10.8 mm. long, the filaments free for 5–6.5 mm., the anther 1.2–1.7 mm. long, 0.6–0.8 mm. wide, oblong, slightly emarginate at both ends; pistil 5.2–5.5 mm. long, the styles filiform, stigmatic for 0.8 mm., free for 2–2.2 mm., united for 1–1.2 mm., the ovary ovoid to ellipsoid, the upper half of the ovary and base of the styles tomentose-sericeous, hairs forked and stellate, 0.2–1.3 mm. long, stipe none.

Fruit not seen.

Flowering specimens collected from September to November.

TYPE LOCALITY: Sertão near Olho d'Agua, Minas Gerais, Brazil, isotype cited below.

DISTRIBUTION: In herbaceous fields in the desert part of Minas Gerais, Brazil.

BRAZIL: MINAS GERAIS: Near Olho d'Agua, *St.-Hilaire* (P, isotype, also US neg. 5661); F neg. 35382 ex P of type or isotype. Rico Pares?, *Vincent* 818 (L).

The position of the inflorescence, often leaf-opposed, and the relatively long attachment of the petals to the staminal tube indicate that this species belongs to the section *Pyramis*. *M. lanata* var. *inclusa* St.-Hil. appears to be the longistylous form of the species. The species appears to be closest to *M. caracasana* Jacq., but differs considerably from it in vestiture.

49. Melochia tomentosa L. Syst. ed. 10, 1140. 1759.

Usually a shrub or subshrub, rarely an herb, 0.3–4.0 meters high, slender, erect or spreading, usually branched, sometimes several branches from the base, perennial, sometimes flowering the first year, the root sometimes thicker than the base of the stem, the bark of the stem blackish or purplish, the young stems and petioles tomentulose,

usually canescent, hairs stellate, 0.1–0.2 mm. long, internodes 0.8–5.5 cm. long; stipules sometimes deciduous, 2–9 mm. long, 0.4–1.5 mm. wide, deltoid-acuminate or deltoid-acute to nearly linear, densely tomentulose, sometimes also ciliate, hairs stellate, sometimes also simple and forked, 0.1–0.3 (–0.7) mm. long; petiole 0.3–2.0 (–3.0) cm. long.

Lamina (1.2–) 2–6 (–10) cm. long, 0.7–4.0 (–5.0) cm. wide, ovate to lanceolate, rarely suborbicular, the base rounded, subcordate, rarely also subtruncate or subcuneate, the apex acute to rounded, both surfaces usually tomentulose, sometimes hirtellous, usually canescent, sometimes only the lower, or neither surface canescent, hairs stellate, 0.1–0.5 mm. long, the margin irregularly crenate or crenate-serrate, crenations or serrations 0.7–5.0 mm. wide, 0.3–2.0 mm. high, (5–) 6–9 (–11) pairs of primary veins, usually 2 are basal, the veins impressed above, prominent beneath.

Inflorescences usually axillary, 1.5–5.0 cm. long, sometimes also leaf-opposed, 2–3 cm. long, or terminal, extending 3–3.2 cm. beyond the first leaf, umbellate, 2–10 (–20) flowers per umbel, at (1–) 3–9 upper nodes, sometimes at 2–3 naked nodes, the peduncle 0.3–2.5 (–5.0) cm. long, 0.5–0.6 mm. wide, rarely with a branch 0.5 cm. long, rarely two in an axil, the pedicel 2–5.7 mm. long; bracts 1–6.1 mm. long, 0.1–0.7 mm. wide, shape and pubescence like those of the stipules.

Calyx green, rarely dull red distally, 4.9–8.6 mm. long, 3.2–7.0 mm. wide, densely tomentulose, canescent, hairs stellate, sometimes also glandular, 0.1–0.3 mm. long, the teeth 2.8–5.8 mm. long, 0.7–2.2 mm. wide, deltoid or ovate, acute or acuminate, the sinus acute to rounded; petals purple, pink, violet, blue, sometimes paler proximally, rarely red or white, 8–13.5 (–17) mm. long, 2.0–3.8 (–6.4) mm. wide, oblanceolate- to obovate-cuneate and spatulate, attached to the stamens for 2.8–5.4 mm., the claw 1.7–3.0 mm. long, sometimes united for 2 mm.

Longistylous form. Stamens 4–6.5 (–9.0) mm. long, the filaments free for 1.8–2.7 mm., the anther 1.1–1.2 mm. long, 0.6–0.8 mm. wide, oblong, emarginate at both ends; pistil 7–10.9 (–12) mm. long, the styles free for 3.2–6.0 mm., united for 3 mm., papillose and slightly clavate for 0.7–1.5 mm. at the apex, the ovary and usually the base of the styles tomentulose, hairs stellate, 0.1–0.4 mm. long, the ovary ellipsoid to ovoid, the stipe 0–1 mm. long.

Brevistylous form. Stamens 7–12.2 mm. long, the filaments free for 2.5–6.3 mm., the anther 0.9–1.5 mm. long, 0.5–0.9 mm. wide; pistil 4.5–5.5 (–8.0) mm. long, the styles free for 1.5–2.6 mm., united for 1.5–3.0 mm., papillose for 0.4–1.0 mm. at the apex, the ovary

and base of styles densely tomentulose, hairs stellate, 0.1–0.6 mm. long, the ovary ellipsoid, the stipe 0–2 mm. long.

Fruit 6.5–10.5 mm. long, 6.6–10.5 mm. wide, long-rostrate, the rostrum 1.3–5.0 mm. long, pyramidal, sometimes suboblong, pentaterous, the lateral points of wings at or below the middle of the fruit, rather short, acute or rounded, the sulci extending a third to half way to the center of the fruit, the base of the fruit narrowed into a stipe 1–1.5 mm. long, tomentulose, hairs stellate, forked, 0.1–0.6 mm. long; dehiscence loculicidal all along the dorsal and ventral sutures, eventually also septicidal; seeds 2–3 mm. long, 1.1–2.0 mm. wide, obovate, red-, purple-, chocolate-, or light-brown, sometimes longitudinally striate, sometimes canescent at the ends and along the raphe, 1 or 2 per cell.

Flowering and fruiting specimens collected throughout the year.

Key to Varieties of *M. tomentosa*

1. Lamina green on both surfaces, hispidulous; petals often large, sometimes 15–17 mm. long; plant very slender; inflorescences at few nodes.
   49d. M. tomentosa var. **speciosa**
1. Lamina canescent and tomentulose at least on the lower surface; petals up to 13.5 mm. long; plant usually robust; inflorescences often at many nodes.
   2. Upper surface of lamina green, lower canescent, serrations relatively few and broad . . . . . .**49c. M. tomentosa** var. **turpiniana**
   2. Upper and lower surfaces of lamina canescent, serrations relatively numerous and narrow.
      3. Leaves medium-sized, lamina typically 2–6 cm. long, 0.7–4.0 cm. wide, petiole often more than 1 cm. long.
         49a. M. tomentosa var. **tomentosa**
      3. Leaves small, lamina typically 1–3 cm. long, up to 2 cm. wide, petiole less than 1 cm. long; stems much more branched and canescent for a shorter distance from the apex than in the typical variety.
         49b. M. tomentosa var. **frutescens**

49a. Melochia tomentosa L. var. **tomentosa**

Melochia crenata Bert. ex. Spreng. Syst. 3:29. 1826; not Vahl 1794.
Melochia portoricensis Spreng. Syst. 3:29. 1826.
Melochia plicata Presl, Rel. Haenk. 2:145. 1835.
Melochia hypoleuca Miq. Linnaea 22:468. 1849.
Ridleia hypoleuca (Miq.) Walp. Ann. 2:166. 1852.
Melochia tomentosa L. var. *typica* Schum. *in* Mart. Fl. Bras. 12(3):34. 1886.
?*Melochia tomentosa* L. var. *Bahiensis* Schum. *in* Mart. Fl. Bras. 12(3):34. 1886.
Melochia arida Rose, Contr. U.S. Nat. Herb. 8:321. 1905.
Moluchia tomentosa (L.) Britt. Brooklyn Bot. Gard. Mem. 1:69. 1918.
Sida rajoides M. E. Jones, Extracts from Contr. West. Bot. 18:58. 1933.

The leaves of the typical variety are tomentose and canescent on both surfaces. The lamina is typically 2–6 cm. long and 0.7–4.0 cm. wide.

TYPE LOCALITY: Jamaica. There are two specimens of *M. tomentosa* in the Linnaean herbarium. One appears to be *M. tomentosa* var. *tomentosa* and the other *M. tomentosa* var. *frutescens*. Localities of collections are not given.

DISTRIBUTION: Southern Florida, southern Texas to Nicaragua, West Indies, Venezuela, Colombia, Surinam, and northeastern Brazil to Bahia, usually in dry, open places, on rocky limestone hills, in coastal thorn thickets, savanna, pineland, along the roadside, in granite sand, in loam, on volcanic slopes, at 0–1,250 meters elevation, usually below 500 meters.

UNITED STATES: FLORIDA: DADE: Buena Vista, *Small* 7268 (S, US). TEXAS: HIDALGO: Mission, *Shiller* 644 (US).

MEXICO: S. Augustin, *Liebmann* 11880 (US). LOWER CALIFORNIA: Cerralvo, *Rose* 16889 (US). Loreto, above Primiera Agua, *Jones* 27167 (US), 27170 (US). Aguaje de San Esteban 25 mi. N. of San Ignacio, *Nelson & Goldman* 7205 (US). About 5–10 mi. W. of San Ignacio, *Wiggins* 5443 (MICH, US); *Thomas* 8330 (US). About 26–27 km. NW. of San Ignacio, *Carter et al.* 1967 (US), 2519 (US). Forty mi. E. of San Ignacio, *Shreve* 7056 (MICH). From Agua Colorado to Cerro Colorado, *Nelson & Goldman* 7321 (US). Carmen Island, *E. Palmer* 823 in 1890 (US). Isla Partida, *Collins et al.* 150 (US). North of Comondu, *Wiggins* 5476 (MICH, US). Forty mi. NE. of Pozo Alemán, *Wiggins* 7817 (US). Northeast of Pozo Alemán, *Shreve* 6984 (MICH). Two mi. E. of Pozo Alemán, *Epling & Robinson* s.n. (MICH). About 28 mi. S. of Pozo Alemán, *Wiggins* 7876 (US). San Jose de Magdalena, *Wiggins* 11381 (US). Magdalena Island, *Brandegee* s.n. (US); *Orcutt* 46 (US). San Nicholas Bay, *Johnston* 3734 (US). Puerto Escondido, *Johnston* 3853 (US). Ceralbo Island, Gordas Point, *Johnston* 4033 (US). La Paz and vicinity, *Collins et al.* 56 (US), 60 (US); *E. Palmer* 121 in 1890 (US); *Hammerly* 208 (US); *Shreve* 7201 (MICH). Between La Paz and Santo Domingo, *Thomas* 8452 (US). Between Santonio and Puerto de Bahia de los Muertos, *Wiggins* 5637 (MICH, US). Todos Santos, *Jones* 24108 (MICH). San José del Cabo and vicinity, *Brandegee* s.n. (US); *Thomas* 7761 (US); *Purpus* 318 in part (US); *Carter et al.* 2194 (US); *Dawson* 1191 (MICH). Cape San Lucas, *Rose* 16360 (US); *Xantus* 13 (US). SONORA: Guaymas, *Rose et al.* 15015 (GH, US); *Rose* 1205 (US, type of *Melochia arida* Rose); *Drouet & Richards* 4029 (MICH); *Gentry* 4714 (MICH). Bahia San Carlos, *Dawson* 1062 (MICH). TAMAULIPAS: *Viereck* 641 (US). Matamoros, *Runyon* 423 (US). Buena Vista Hda., *Wooton* s.n. (US). San Miguel La Tamaulipeca, *Bartlett* 10585 (MICH), 10679 (MICH, US). El Limon, *Kenoyer & Crum* 3637 (MICH). Victoria, *Leavenworth* 240 (GH). SINALOA: Vicinity of Culiacan, *Ortega* 6691 (US). Altata, *Gentry*, 5437 (MICH). DURANGO: *Rose* 2272 (US). ZACATECAS: San Juan Capistrano, *Rose* 2413 (US). SAN LUIS POTOSÍ: Las Palmas, *Rose & Hough* 4880 (US). Valles, *Kenoyer* s.n. (MICH). NAYARIT: TRES MARIAS ISLANDS: Maria Madre Island, *Nelson* 4205 (US); Tepic, Cañon de Jesus Maria, *Goldsmith* 145 (GH). VERA CRUZ: Zacuapan, Barranca de Santa Maria, *Purpus* 2357 (US); *Rozynski* 608 (R). Baños del Carrizal, *Purpus* 6134 (US). PUEBLA: San Luis Tultitlanapa near Caxaca, Rio de Santa Lucia, *Purpus* 2612 (US). MICHOACÁN: APATZINGAN: Tiquiluca, *Hinton* 12121 (US). COLIMA: *E. Palmer* 956 in 1891 (MICH, US). GUERRERO: Acapulco and vicinity, *Bailey* 514 (MICH); *Haenke* (PR 174399a, b, c, type of *Melochia plicata* Presl, also US neg. 5550, W, isotype); *E. Palmer* 258 in 1894–95 (MICH, US). OAXACA: Near Tomellin, *Rose et al.* 10083 (US).

Tomellin Canyon, *J. N. & J. S. Rose* 11330 (US). Estacion Almoloyas, Cañon de Tomellin, *Conzatti* 1685 (US), 2034 (MICH). Playa de Coyula, *Reko* 3664 (US). "Cancatlan" (?Cuicatlán), *Rusby* 64 (US). Vicinity of San Juan Guichicovi, *Nelson* 2716 (US). Ixtepec, *Fisher* 35467 (US). San Geronimo, *Mell* 2111 (US), 2147 (MICH). Cuicatlán, *Gonzalez* 978 (US). Estacion de Quiotepec, *Conzatti* 4588 (US). Salina Cruz and vicinity, *King* 209 (MICH); *Deam* s.n. (MICH). Tehuantepec and vicinity, *Matuda* 923 (MICH); *King* 862 (MICH), 441 (MICH), 346 (MICH). About 5.5 km. NE. of Juchitán, *King* 364 (MICH). CAMPECHE: Konchen, *Lundell* 1388 (MICH). YUCATÁN: Balantun, *Gaumer* 23267 (US). Chichankanab, *Gaumer* 1799 (US). Mérida, *Collins* 13 (US); *Souza Novelo* 259 (US). Progreso, *Steere* 3029 (MICH). Muna, *Steere* 2136 (MICH). QUINTANA ROO: Coba on bank of aguada W. of Lake Coba, *C. L. & A. A. Lundell* 7670 (MICH, US).

HONDURAS: CORTES: Rio Lindo, *Edwards* P-698 (US).

NICARAGUA: MANAGUA: Managua and vicinity, *Garnier* 1168 (MICH, US); *Chaves* 72 (US). GRANADA: Granada, *Baker* 213 (MICH).

BAHAMAS: Eleuthera, Harbor Island, *E. G. Britton* 6387 (US). NEW PROVIDENCE: Near Nassau, *Curtiss* 12 (L, US). ANDROS: Coppice, Smith Hill, Long Bay Cays, *Small & Carter* 8666 (US). EXUMA CHAIN: Great Guana Cay, *Britton & Millspaugh* 2877 (US).

CUBA: CAMAGÜEY: Vicinity of Pueblo Romano Cayo Romano, *Shafer* 2437 (US). Six mi. from NE. end of Cayo Coco, *Shafer* 2728 (US). Paloma, Cayo Sabinal, *Shafer* 816 (US). Cayo Guajaba, *Shafer* 640 (US). ORIENTE: Northward of Raimon, Nipe Bay, *Shafer* 1784 (US). Santiago and vicinity, *Taylor* 17 (US). *Lopez Figueiras* 189 (US). Siboney, *Morton* 3970 (US). Yateritas, Via Azul, *Bro. Alain & Morton* 4949 (US). Manigua costera, en el Socucho, Playa de Puerto Padre, *Lopéz F* 2906 (US).

HAITI: Port-au-Prince and vicinity, *Leonard* 2816 (US); *Bailey* Haiti 132 (US), Haiti 283 (US). TORTUE ISLAND: Vicinity of La Vallée, *E. C. & G. M. Leonard* 11647 (MICH, US), 15406 (US). GONAVE ISLAND: Pte. à Raquette, *Eyerdam* 223 (US). Vicinity of Étroite and Anse Galette, *Leonard* 3112 (US), 3351 (US). Gonaïves and vicinity, *Nash & Taylor* 1546 (US); *Buch* 283 (L, S); *Leonard* 10061 (US). Vicinity of St. Raphael, *Leonard* 7692 (US). Vicinity of Jean Rabel, *E. C. & G. M. Leonard* 13829 (US). Vicinity of Mole St. Nicholas, *E. C. & G. M. Leonard* 13210 (US). Vicinity of Cabaret, *E. C. & G. M. Leonard* 12016 (US). Vicinity of Fond Parisien, Etang Saumatre, *Leonard* 4117 (US), 4132 (US). Vicinity of St. Marc, *Leonard* 2876 (US).

DOMINICAN REPUBLIC: *C. Wright et al.* 45 (US), 108 (US). Azua, *Rose et al.* 4024 (US). SANTIAGO: Guayacanal, *Jiménez* 2263 (US). MONTE CRISTI: Guayubin, *Abbott* 941 (US). BARAHONA: *Fuertes* 382 (US).

JAMAICA: Kingston and vicinity, *Killip* 11 (US); *Maxon & Killip* 1385 (US), 308 (US). Near Falmouth, *W. Harris* 7222 (US). Near Alligator Pond, *W. Harris* 7230 (US). Watsons Hill, *W. Harris* 6315 (US). Long Mountain Road, *Fawcett* 7313 (US). East slope of Hellshire Hills, *Proctor* 7502 (US). Port Henderson, *J. A. Harris & Lawrence* C1537 (US). GRAND CAYMAN ISLAND: *Proctor* 15054 (IJ).

PUERTO RICO: Cayo Muertos, *Britton et al.* 4971 (US). San Ildefonzo, *Goll et al.* 701 (US). Coamo, *Sintenis* 3150 (US).

LESSER ANTILLES: U.S. VIRGIN ISLANDS: ST. CROIX: Bassin, *Ricksecker* 127 (US). ST. JOHN: Near Lamosure, *Britton & Shafer* 644 (US). MARTINIQUE: *Duss* 1360 (US). *H. & M. Stehlé* 6861 in part (US). *Sieber* 321 (L). Case Pilote, *Hahn* 248 (GH, L, US), 240 (R). GRENADA: St. George, *Broadway* in 1896 (US).

DUTCH WEST INDIES: CURAÇAO: Various localities, *Suringar*, Jan. 1885 (L). Near Willemstad, *Britton & Shafer* 2913 (US). BONAIRE: *Suringar* Feb. 20–23, 1885 (L). Rincon, *Boldingh* 7010 (L). ARUBA: Koolwijk, *Suringar* Jan.-Feb. 1885 (L).

TRINIDAD: Patos Island, *Broadway* 2716 (S).

VENEZUELA: Valley of Puerto La Cruz, Hacienda Panarigua, *Pittier* 9199 (US). NUEVA ESPARTA: MARGARITA ISLAND: El Valle, *Miller & J. O. Johnson* 44 (US). SUCRE: Vicinity of Cristóbal Colón, *Broadway* 133 (US). FEDERAL DISTRICT: Around Caracas, *Pittier* 6170 (US). Lower Cotiza, near Caracas, *Pittier* 7257 (US). Vicinity of Cabo Blanco, *Pittier* 10274 (US). La Guaira, *Curran & Harman* 846 (US), 876 (US). Catia de la Mar, *Tamayo* 399 (US); *Vogl* 617 (S). ARAGUA: Colonia Tovar, *Fendler* 107 (US). CARABOBO: El Palito, on road from Valencia to Puerto Cabello, *Pittier* 7668 (US). FALCÓN: Paraguaná, Pueblo Nuevo, *Tamayo* 1033 (US). MÉRIDA: Brecenio Hacienda 23 mi. SE. of Mérida, *Reed* 547 (US). Vallée du Rio Chama, en aval d'Egido, *Humbert* 26537 (P, US). BOLÍVAR: Ciudad Bolívar, *Holt & Gehriger* 85 (US), 100 (US); *L. H. & E. Z. Bailey* 1508 (US).

COLOMBIA: MAGDALENA: Santa Marta, *Curran* s.n. (US). Near Fonseca, *Haught* 4311 (US). Cerrejón, *Haught* 6639 (US). ATLÁNTICO: Barranquilla, *Bro. Elias* 134 (US). BOLÍVAR: Vicinity of Cartegena, *Bro. Heriberto* 9 (US). NORTE DE SANTANDER: Vicinity of Cúcuta, *Killip & Smith* 20981 (US); *Molina & Barkley* 18 N. S. 011 (US).

BRAZIL: PIAUÍ: Sete Lagoas, *Lützelburg* 1476 (RB). CEARÁ: Motuquinha, *Löfgren* 460 (R, S). PARAÍBA: *de Moraes* 804 (US). PERNAMBUCO: Petrolandia, *Kuhlmann* s.n. (RB). Alagôa de Baixo, *Monteiro* 238 b (R). Caruarú (Carapotoz), *Pickel* 3511 (US). ALAGOAS: *Gardner* 1258 (S, US). BAHIA: Jacobina, *Schreiner* s.n. (R). Joazeiro, *Löfgren* 961 (RB). Joazeiro, Horto Florestal, *Zehntner* 148 (R). Frageiro, Rio S. Francisco, *Zehntner* 768 (M). Queimadas, *Rose & Russell* 19836 (US).

This species is related to *Melochia pyramidata L.* The fruit of the latter is not as hairy, and is frequently purple blotched. Also, the fruit of *M. tomentosa* has a longer rostrum and the lateral angle of the wings is acute or rounded, but is acute or acuminate in *M. pyramidata*. *Melochia tomentosa* is usually a taller and hairier plant than *M. pyramidata*. The leaves of *M. pyramidata* are usually subglabrous and usually have some simple hairs on the upper surface, those of *M. tomentosa* are usually tomentose and canescent and do not have simple hairs. The inflorescences of *M. pyramidata* are usually leaf-opposed, those of *M. tomentosa* are usually axillary.

The flowers open in the morning and close in the afternoon (Runyon), and are very fragrant (*M. arida* Rose) (Rose).

The varieties of *M. tomentosa* grade into one another.

49b. Melochia tomentosa L. var. **frutescens** (Jacq.) DC. Prodr. 1:490. 1824.
Melochia frutescens Jacq. Obs. Bot. 2:22, pl. 44. 1767.
Moluchia frutescens (Jacq.) Medic. Malv. 10. 1787.

The leaves of this variety are smaller than those of the typical variety. The petiole is less than 1 cm. long, and the lamina is typi-

cally 1–3 cm. long and less than 1 cm. to 2 cm. wide. The stem branches more than that of the typical variety.

TYPE LOCALITY: Saint Martin, West Indies.

Distribution: Mexico, West Indies, Venezuela, and Colombia.

MEXICO: LOWER CALIFORNIA: San Francisquito Bay, *Rose* 16733 (US); *Johnston* 3568 (US). Espiritu Santo Island, the Isthmus, *Johnston* 3962 (US). NAYARIT: TRES MARIAS ISLANDS: Maria Madre Island, *Maltby* 57 (US); *Solis* 12 (US). OAXACA: Puerto Angel, *Morton & Makrinius* 2641 in part (US). Teotitlán del Camino, *Seler* 809 (US).

BAHAMAS: ELEUTHERA: Rock Sound, *Krebs* s.n. (S). ?Siklins Island, *Eggers* s.n. (S). ANDROS: Mangrove Bay, *Brace* 4907 (US).

TURKS and CAICOS: *Proctor* 8780 (IJ), 9177 (IJ).

CUBA: *C. Wright* 40 (S, US). CAMAGÜEY: Pastelillo, Cayo Sabinal, *Ekman* 15413 (S), 15536 (S). ORIENTE: Santiago de Cuba W. of Playa Siboney, *Ekman* 7748 (S), 8730 (S). Guantánamo at Caimanera, *Ekman*, 2866 (S). Guantánamo Bay, *Britton* 1948 (US). Vicinity of El Cobre, *Pollard & W. Palmer* 384 (US). Berraco, vicinity of Daiquiri, *Britton & Cowell* 12672 (US); *Maxon* 4028 (US).

HAITI: Port de Paix, *Ekman* 3837 (S). Vicinity of St. Michel de l'Atalaye, *Leonard* 7327 (US), 7335 (S, US). Vicinity of Ennery, *Leonard* 10025 (US). Gonaïves and vicinity, *Leonard* 10067 (US). Vicinity of Cabaret, *E. C. & G. M. Leonard* 11874 (US), 11936 (US).

DOMINICAN REPUBLIC: Near Manuel de Ocoa, *Türckheim* 3690 (L, S, US). Monción, *Valeur* 158 (S, US). Gurabito, *Eggers* 1991 (US). MONTE CRISTI: Near Rio Yaque del Norte, *R. A. & E. S. Howard* 9608 (US), 9619 (US). BARAHONA: Trujín, *Abbott* 1726 (US). La Salina, *R. A. & E. S. Howard* 8364 (US). Beata Island, *Howard* 12498 (S, US); *Jiménez* 3772 (US).

JAMAICA: Kingston, *Orcutt* 4956 (S).

PUERTO RICO: *Stahl* 1027 (L, S). *Wydler* 26 (S). Cabo Rojo, Las Salinas, *Otero* M–33 (MICH); *Sintenis* 628 (L, S, US). Morrillos de Cabo Rojo, *Britton et al.* 4715 (US). Ponce and vicinity, *Underwood & Griggs* 698 (US); *Heller* 482 (US), 6064 (L, US). Coamo Springs, *Underwood & Griggs* 562 (US). Guanica, *Sintenis* 3499 (US). Brigadier Point to Puerto Negro, *Shafer* 2921 (US). ?La Paguera, *Sargent* 155 (US). ?Tajarto, *Sintenis* 1602 (US).

LESSER ANTILLES: U.S. VIRGIN ISLANDS: ST. CROIX: *Benker* s.n. (S). Salt pond, *Raunkiaer* s.n. (S). *Hansen* 109 (L). Frederiksted, *Rose et al.* 3525 (US), 3226 (US). ST. THOMAS: *Oersted* collected 1845–48 (MICH, S, US). *Schomburgk* 42 (W). *Eggers* 49 (US), 96 (MICH), 194 (S), 262 (L). *Wydler* s.n. (L). Water Island, *Britton et al.* 108 (US). ST. JOHN: *Breutel* s.n. (L). BRITISH VIRGIN ISLANDS: Tortola, *Fishlock* 43 (US). ST. MARTIN: *Suringar* May 1, 1885 (L). ST. BARTHÉLEMY: *Forsström* s.n. (S), *Euphrasén* s.n. (S), *von Goes* s.n. (S). St. Jean, *Stehlé* 911 (US). ST. EUSTATIUS: *Suringar* Apr. 8, 1885 (L). ST. KITTS: Canada Estate, *Britton & Cowell* 740 (US). ANTIGUA: Slopes and summit of Boggy Peak, Shekerley Mts., *A. C. Smith* 10421 (S, US). Near English Harbor, *Rose et al.* 3357 (US). Lyons, *Box* 997 dupl. (US). MONTSERRAT: *Shafer* 418 (US). GUADELOUPE: *Duss* 480 (US), 2901 (US). GRENADINES: West coast of Mustique, *A. C. Smith* 10163 (S, US).

CURAÇAO: *Killip & Smith* 21056 (US). *Curran & Haman* 26 (US).

TRINIDAD: Patos Island, *Britton et al.* 526 (US).

VENEZUELA: Northern Venezuela, *Curran & Haman* 876 (US). NUEVA ESPARTA: Robledar, *Gines* 3191 (US), 3871 (US). El Valle, *Gines* 4126 (US). R. Matasiete, *Gines* 2759 (US), 3195 (US). Salamanca, *Gines* 3647 (US). Cer-

rado, *Gines* 3768 (US). SUCRE: Valley of Bordones SW. of Cumaná, *Steyermark* 62891 (US). LARA: Barquisimeto, *Tamayo* 2616 (US). Carora, *Jahn* 184 (US). TRUJILLO: La Conception, *Reed* 1011 (US). MERIDA: El Molino, just above Lagunillas, *Steyermark* 56222 (US). BOLIVAR: Along Río Caroní, near Puerto Ordaz, *Steyermark* 94224 (US).

COLOMBIA: MAGDALENA: Near Codazzi, about 90 km. NE. of Chiriguaná, *Haught* 2306 (MICH, US), 3734 (US).

49c. Melochia tomentosa L. var. **turpiniana** (H.B.K.) Schum. *in* Mart. Fl. Bras. 12(3):34. 1886.

Melochia Turpiniana H.B.K. Nov. Gen. & Sp. 5:323, pl. 482. 1823.

The leaves of this variety are about the size of those of the typical variety, but differ in that the upper surface is green rather than canescent and the serrations are broader and fewer.

TYPE LOCALITY: ?Colombia. The type was collected by Humboldt and Bonpland who were not certain of the locality.

DISTRIBUTION: Mexico, West Indies, Venezuela, and Colombia.

MEXICO: Mexico und Umgebung, *Wawra* 394 (W). JALISCO: Tequila, *Herrerón* Nov. 1902 (S). Corcovado Canyon, NE. of Autlán, toward Guadalajara, *R. L. & C. R. Wilbur* 2378 (MICH, US). MICHOACÁN: Zitacuaro-Tuzantla, *Hinton* 13064 (US). Between San Juan de los Plátanos and Amatlán, *McVaugh*, 17956 (MICH, US). COLIMA: Manzanillo and vicinity, *Ferris* 6150 (US). OAXACA: Tomellin Canyon, *Pringle* 4631 (MICH, S, US). About 4–5 km. E. of Juchitán, *King* 1631 (US). YUCATÁN: *Gaumer* 487 (MICH, S, US). QUINTANA ROO: Cozumel Island, *Gaumer* 88 (K).

HAITI: Port-au-Prince and vicinity, *Ekman* H. 9342 (S, US); *Rose* 22096 (GH, US); *Holdridge* 1005 (MICH, US).

DOMINICAN REPUBLIC: Santo Domingo, Valle del Cibao, *Ekman* H. 15983 (S).

JAMAICA: *Swartz* s.n. (S). *D. D. Wright* s.n. (S).

LESSER ANTILLES: MARTINIQUE: Near Casa Pilote, *Hahn* 240 (S). GRENADINES: Bequia, *Eggers* 7058 (US). Cannovan I., *Beard* 1409 (S, US).

VENEZUELA: ANZOÁTEGUI: Puerto La Cruz, Guaraguao, *Pittier* 14909 (US). CARABOBO: Puerto Cabello, *Linden* 1549 (W). LARA: Near Barquisimeto, *Saer* 233 (US).

COLOMBIA: *Wagener* 32 (US). ?COLOMBIA: *Humboldt & Bonpland*, F neg. 35386 ex P of type of *Melochia Turpiniana* H.B.K. (US). MAGDALENA: Around Rio Frío, between the Cienaga de Santa Maria and the foothills, *Pittier* 1601 (US). Santa Marta, *H. H. Smith* 474 (L, S, US). ATLÁNTICO: Barranquilla and vicinity, *Bro. Elias* 186a (US); *Torregroza et al.* 18 At 505 (US); *Dugand* 3254 (US); *Bro. Paul* C–2 (US). Near Puerto Colombia, *Kattáh et al.* 19 At 033 (US); *Bro. Elias* 24 (US), 824 (US). BOLÍVAR: Cartagena and vicinity, *Billberg* 33 (S); *Engstedt* 45 (S); *Dahlin* s.n. (S); *Killip & Smith* 14017 (US), 10462 (US).

49d. Melochia tomentosa L. var. **speciosa** (S. Wats.) A. Goldberg, comb. et stat. nov.

Melochia speciosa S. Wats. Proc. Amer. Acad. 24:42. 1889.

Melochia pterocarpa J. Ar. *in* Mém. Inst. Sci. Madag., ser. B, 7:68. 1956.

The leaves of this variety are small and differ from those of the other varieties in being green on both surfaces and hispidulous rather

than tomentulose. The plant is very slender, has inflorescences at few nodes, and the flowers are larger than average for the species.

The zygomorphy of the corolla and androecium reported by Arènes for his *M. pterocarpa* may have been due to differential shrinkage in drying or to an anomalous condition. I dissected flowers from the type specimen and found petal sizes intermediate between the extremes reported by Arènes. The range in length of petals from one corolla was 13.3–14.4 mm. The calyx teeth of *M. tomentosa* may vary slightly in size in a single calyx.

TYPE LOCALITY: The type was collected by *E. Palmer*, no. 650, at Guaymas, Sonora, Mexico, and is cited below.

DISTRIBUTION: Endemic to Western Mexico, adventive in Madagascar.

MEXICO: SONORA: Guaymas, *E. Palmer* 148 in 1887 (MICH, US), 266 in 1897 (S, US), 650 in 1887 (US, type of *Melochia speciosa* S. Wats.). Three mi. W. of Jori, *Pennell* 19458 (US). SINALOA: Vicinity of Culiacan, *Brandegee* s.n. (US). Vicinity of Topolobampo, *E. Palmer* 205 in 1897 (MICH, US); *Rose et al.* 13275 (US). Cerros del Fuerte, 18–24 mi. N. of Loc Mochis, *Gentry* 14288 (US). ZACATECAS: San Juan Capistrano, *Rose* 3551 (US). JALISCO: Near Huejuquilla, *Rose* 3558 (US). MICHOACÁN: Zitacuaro-Tuzantla, *Hinton* 13064 (MICH, US).
MADAGASCAR: *Scott Elliot* 650 (P), type of *M. pterocarpa* J. Ar.

50. Melochia crenata Vahl, Symb. 3:86, pl. 68. 1794.
Riedleia crenata (Vahl) DC. Prodr. 1:491. 1824.
Visenia crenata (Vahl) Spreng. Syst. 3:30. 1826.
Melochia diffusa Bert. ex Spreng. Syst. 3:30. 1826.

A sparingly branched prostrate subshrub or herb with shoots to 1 meter long, the young stems and petioles densely tomentose, somewhat canescent, hairs stellate, 0.3–1.3 mm. long, internodes 2.3–8.3 cm. long; stipules 2.5–3.7 mm. long, 0.8–2.0 mm. wide, ovate to lanceolate, acute, mostly ciliate, hairs simple, 0.3–1.0 mm. long, shorter stellate hairs 0.3–0.5 mm. long on the abaxial surface; petiole 0.7–2.0 cm. long.

Lamina 1.4–3.5 cm. long, 1.1–2.6 cm. wide, oval to broadly ovate, the base rounded, rarely slightly cuneate, the apex rounded, one side sometimes slightly larger than the other, both surfaces densely tomentose, somewhat canescent, velvety to the touch, hairs stellate, 0.1–0.4 mm. long, the margin irregularly crenate-serrate, serrations 1.3–3.5 mm. wide, 0.5–1.1 mm. high, 6–7 pairs of primary veins, 2 basal.

Inflorescences 2.0–3.7 cm. long, 90° from the leaf to leaf-opposed, at 2–9 nodes, the peduncle 0.7–2.1 cm. long, 1 or 2 at a node, terminated by a 2–5-flowered umbel, the pedicel 4.0–7.0 mm. long; bracts 1.0–4.5 mm. long, 0.4–0.8 mm. wide, lanceolate or deltoid- to ovate-acute, mostly ciliate, hairs simple, forked, and stellate, 0.3–1.0 mm. long.

Calyx 5.2–6.2 mm. long, 4.2–5.2 mm. wide, densely tomentose, hairs stellate, 0.3–1.0 mm. long, the teeth 3.0–3.6 mm. long, 1.5–1.9

mm. wide, deltoid-acute to deltoid-acuminate, the sinus acute; petals purple, magenta to rather pale red, 11.2–15.5 mm. long, 3.6–5.2 mm. wide, obovate-cuneate, sometimes with scattered, mostly ciliate, glandular hairs 0.05 mm. long, attached to the stamens for 2.5–3.3 mm., the claw 1 mm. long.

Longistylous form. According to Fawcett & Rendle (13), stamens 7–8 mm. long, the filaments free for 2.5–3.0 mm.; pistil about 11 mm. long, the styles united shortly (1.5–2 mm.) at the base, the ovary and styles somewhat hirsute with branched hairs.

Brevistylous form. Stamens 10.4–11.3 mm. long, the filaments flattened, 0.3 mm. broad, free for 5.5–6.5 mm., with scattered glandular hairs 0.05 mm. long, the anther 1.3–2.0 mm. long, 0.6–0.8 mm. wide, oblong, slightly emarginate at both ends; pistil 4.5–6.9 mm. long, the styles free for 2.1–3.0 mm., united for 0.5–1.0 mm., filiform, papillose for 0.7–0.8 mm., the ovary narrowly ovoid, the united part of styles and ovary hirsute-tomentose, hairs 0.5 mm. long.

Fruit 10.0–10.5 mm. long, of which the rostrum is 1.5–2.0 mm. long, 6.7–8.7 mm. wide, pentapterous-ovate, narrowed at the base to a stripe 0.5–1.0 mm. long, the outer angles of wings rounded, hardly evident, below the middle of the capsule, the sulci between the carpels extending a third to half way to the center of the fruit, densely tomentose, hairs stellate, 0.2–0.5 mm. long; dehiscence loculicidal along the dorsal suture; seeds not quite ripe, 2.9–3.0 mm. long, 1.7–2.0 mm. wide, brown, usually 2 per cell.

Flowering specimens collected in July, September, and October; fruiting ones, in July and October.

TYPE LOCALITY: Near Santa Marta, Colombia. Type collected by von Rohr.

DISTRIBUTION: Colombia and Jamaica in sandy soil near sea level.

?JAMAICA: ?*W. Wright* (W).

COLOMBIA: GOAJIRA: *Dawe* 532 (US). MAGDALENA: Santa Marta, *H. H. Smith* 473 (K, P, S, US), 475 (A). F neg. 21602 of type ex C (US). ?Santa Marta, *Balbis* (S). Riohacha, *Haught* 4409 (US).

The species can be distinguished from other members of the section by its fruits, which are not pyramidal and have rounded rather than acute or acuminate wings. Its trailing habit, leaves rounded at the apex, and long pedicels are also aids in identification. It is perhaps most closely related to *M. tomentosa* L.

The collection of the specimen photographed as F 21602 ex C is attributed to Ryan, but the type was collected by von Rohr.

This species is cited as occurring in Peru by Macbride (39). To my knowledge, it does not occur there.

51. Melochia pyramidata L. Sp. Pl. 674. 1753.

A slender erect or spreading annual or perennial herb to shrub, 0.08–2.0 meters high, usually branched, sometimes several branches from the base of the stem, the root sometimes thickened and 0.5–1.3 cm. wide, the young stems hirsute-tomentulose, hairs in a longitudinal line or surrounding the stem, simple, sometimes also stellate and forked, 0.2–0.5 mm. long, internodes (0.2–) 2–10 cm. long; stipules 1.5–5.3 mm. long, 0.2–1.0 mm. wide, deltoid-acuminate or lanceolate, rarely linear, hirsute-tomentulose and ciliate, hairs simple, forked, and stellate, 0.2–0.8 mm. long; petiole (0.1–) 0.4–2.0 (–4.7) cm. long, hirsute-tomentulose on the upper surface or all the way around.

Lamina (0.7–) 2–6 (–10.5) cm. long, (0.3–) 0.6–3.0 (–7.7) cm. wide, the upper leaves tending to be lanceolate, the lower ovate, rarely oblong, the base rounded, sometimes cordate or attenuate, the apex acute, acuminate or rounded, the basal leaves usually smaller, sometimes nearly orbicular, the upper surface green, subglabrous or hirsute, hairs simple, appressed, sometimes also forked and stellate, 0.1–1.0 mm. long, the lower surface green, with few hairs on the veins, sometimes slightly yellowish-canescent, or tomentulose, hairs stellate, sometimes also forked, simple, and glandular, 0.1–0.4 (–0.7) mm. long, the margin irregularly crenate-serrate, serrations 0.8–4.4 mm. wide, 0.2–2.0 mm. high, 5–11 pairs of primary veins, 1 or 2 (–3) are basal.

Inflorescences generally leaf-opposed, sometimes 90° from the leaf, rarely also axillary or terminal, 1.3–5.2 cm. long, at (1–) 3–8 upper nodes, umbellate, (1–) 3–8 (–15) flowers per umbel, the peduncle slender, (0–) 0.2–1.6 (–3.3) cm. long, 0.4 mm. wide, rarely branched, the pedicel 1–5 (–6) mm. long; bracts 0.5–3.0 mm. long, 0.2–0.7 mm. wide, deltoid-acuminate, lanceolate or linear, ciliate and hirsute-tomentulose, hairs simple, forked, and stellate, 0.1–0.5 mm. long.

Calyx 3.7–6.2 mm. long, 2.1–4.0 mm. wide, ciliate and hirsute-tomentulose, hairs stellate, and forked, 0.1–0.5 mm. long, the teeth 2–4.9 mm. long, 0.6–1.5 mm. wide, usually deltoid-acuminate, sometimes deltoid-acute, the sinus acute to narrowly rounded; petals usually purple, pink, violet, blue, sometimes yellow proximally, rarely red, white or yellow, (3–) 7–11.5 mm. long, (1.5–) 2.4–3.0 mm. wide, obovate-oblanceolate-spatulate, attached to the staminal tube for 1–3 mm., the claw 0.6–2.5 mm. long, sometimes glandular hairs 0.05 mm. long on the petals.

Longistylous form. Stamens (2.6–) 3.5–6.3 mm. long, the filaments free for 0.7–2.0 mm., the anther 0.7–1.2 mm. long, 0.4–0.6 mm. wide, oblong, emarginate at both ends; pistil 4.3–9.0 mm. long, the styles free for 2–4.8 mm., united for 0.5–2.1 mm., filiform, papillose for 0.6–1.0 mm. at the apex, the ovary ellipsoid, the styles and ovary

hirsute-tomentulose, hairs stellate, 0.1–0.4 mm. long, the stipe 0–0.2 mm. long.

Brevistylous form. Stamens 5.7–7.5 mm. long, the filaments free for 3–4 mm., the anther 1–1.2 mm. long, 0.5–0.6 mm. wide, shape same as that above; pistil 3.7–5.0 mm. long, the styles free for 1.4–2.0 mm., the ovary ellipsoid to oblong-ellipsoid, subglabrous to hirsute-tomentulose, hairs 0.1–0.2 mm. long.

Fruit often with purple blotches, 5–9.5 mm. long, (5–) 6.5–14 mm. wide, the rostrum short, 0–2.1 mm. long, the base narrowed into a stipe 0.2–1.0 mm. long, occasionally 6 or 7 carpels present, pyramidal, pentapterous, the points of wings acute or acuminate, at the middle or toward the base of the fruit, the sulci between the carpels extending half way to the center of the fruit, the base stipitate for 0.2–1.0 mm., subglabrous, hirsute or tomentulose, hairs only stellate or also simple and forked, 0.1–0.5 mm. long; dehiscence loculicidal all along the dorsal and ventral sutures; seeds 1.7–2.6 mm. long, 1.1–1.7 mm. wide, trigonal, brown, 1 or 2 per cell.

Flowering and fruiting specimens collected throughout the year in the West Indies and for 8 months in the colder regions near the extremes of the range.

Key to Varieties of *M. pyramidata*

1. Lamina subglabrous, hairs on upper surface often simple.
51a. M. pyramidata var. **pyramidata**
1. Lamina usually tomentulose beneath, hairs on upper surface more commonly stellate . . . . . **51b. M. pyramidata** var. **hieronymi**

51a. Melochia pyramidata L. var. **pyramidata**

Melochia domingensis Jacq. Select. Stirp. Amer. 194. 1763.
Moluchia fruticosa Medic. Malv. 10. 1787.
Moluchia herbacea Medic. Malv. 10. 1787.
Moluchia domingensis (Medic.) Steud. Nom. II, 2:155. 1841.
Sida Sabeana Buckley, Proc. Acad. Phila. for 1861, 449. 1862.
?*Melochia pyramidata* L. var. *normalis* O. Ktze. Rev. Gen. Pl. 3(2):25. 1898.
Moluchia pyramidata (L.) Britt. Brooklyn Bot. Gard. Mem. 1:69. 1918.

The leaves of the typical variety are subglabrous.

TYPE LOCALITY: Brazil. The type is in the Linnaean herbarium.

DISTRIBUTION: Southern and western Texas to Costa Rica, West Indies, northern South America to northern Argentina, adventive in tropical and subtropical areas in various parts of the world, usually in open disturbed places, often along the roadside, margin of cultivated fields, and in waste places, in various types of wet or dry soil, at 0–1,560 meters elevation, usually below 1,000.

UNITED STATES: TEXAS: Guadalupe River, *Lindheimer* 356 (US, W). Western Texas to El Paso, *C. Wright* 1334 (US). Mexican Boundary Survey, *Parry et al.* s.n. (US). COMAL: Comanche Spring, New Braunfels, *Lindheimer* 687

(US, W). Bracken, *Groth* 110 (US). BEXAR: 25 mi. N. of San Antonio, *Schulz* 554 (US). COLORADO: Eagle Lake, *E. J. Palmer* 6601 (US); *Barkley et al.* 46449 (S, W). GALVESTON: San Leon, *Fisher* 5083 (US). UVALDE: Uvalde, *E. J. Palmer* 12295 (US). KINNEY: Near Rio Grande River, *Correll* 14901 (US). BRAZORIA: Brazos River, *Bush* 271 (US). Columbia, *Bush* 1346 (US). MATAGORDA: Bay City, *Fisher* 180 (US). *E. J. Palmer* 9625 (S, US). Near Colorado River W. of Bay City *Rogers* 6599 (W). Palacios, gulf coast, *Tharp* 178 (MICH). MAVERICK: Eagle Pass, *Havard* s.n. (US). CALHOUN: Guadalupe River bottoms, 15 mi. SW. of Port Lavaca, *Cory* 51145 (US). KLEBERG: Kingsville, *Bogusch* S–130 (US). WEBB: Laredo, *J. N. & J. S. Rose* 11019 (US). Laredo, Rio Grande River, *E. Palmer* 117 in 1879–80 (MICH, US). HIDALGO: Mission, *Shiller* 843 (US). Tabasco, *Clover* 218 (MICH). Six mi. S. of Alamo, *Clover* 879 (MICH). Rio Grande Valley, *M. L. Walker* 41 (S, W). WILLACY: E. of San Perlita, *C. L. & A. A. Lundell* 8782 (MICH). CAMERON: Brownsville, *Hanson* 300 (US); *Rose & Russell* 24245 (US); *Runyon* 554 (US); *Tharp* 1179 (US). Las Palmas Plantation, about 4 mi. SW. of Brownsville, *Correll* 14862 (US). Arroyo Colorado, Olmito road, *Clover* 1261 (MICH).

MEXICO: *Sartorius* s.n. (US). Mirador, *Sartorius* s.n. (US). SONORA: Vicinity of Alamos, *Rose et al.* 12912 (US); *Gentry* 4770 (MICH, US). On road to Guaymas 16 mi. S. of Hermosillo, *Wiggins & Rollins* 205 (MICH). COAHUILA: Sabinas, *Nelson* 6816 (US). About 23 mi. S. of Sabinas, *Shreve* 8418 (MICH, US). Palm Canyon, *Marsh Jr.* 972 (GH). Muzquiz, Santa Anna Canyon, *Marsh Jr.* 444 (GH). Monclova, *White* 1726 (MICH). NUEVO LEON: Rio Santa Catarina, Monterrey, *Bro. Arsène* 6304 (US). About 28 mi. S. of Nuevo Laredo on road to Monterrey, *T. C. & E. M. Frye* 2340 (US). Valley, Monterrey, *Pringle* 1939 (MICH, S, US, W). Forty mi. S. of Laredo, *Schery* 7 (MICH). Mts. near Monterrey, Diente Canyon, *C. H. & M. T. Mueller* 303 (W). TAMAULIPAS: San Lucas, *Viereck* 737 (US), 876 (US). Victoria and vicinity, *E. Palmer* 68 in 1907 (US); *Fisher* 3355 (US). Vicinity of El Mulato near Tanque, *Bartlett* 10996 (MICH, US), 10994 (MICH). Vicinity of Marmolejo, *Bartlett* 10945 (MICH). Buena Vista Hda., *Wooton* s.n. (US). Ten mi. E. of Ciudad Mante, *Kenoyer & Crum* 3665 (MICH). Huisachal, *Stanford et al.* June 29, 1949 (US). SINALOA: Mazatlan and vicinity, *Rose et al.* 13676 (US); *Lamb* 354 (US); *Brandegee*, Oct. 8, 1893 (UC). Culiacan, *Rose et al.* 14856 (US); *Brandegee*, Sept. 19, 1904 (UC). Vicinity of Villa Union, *Rose et al.* 13929 (US). Vicinity of Topolobampo, *Rose et al.* 13274 (US). Imala, *Gentry* 4944 (MICH). SAN LUIS POTOSÍ: Tamasopo, *Fisher* 3735 (US). Tancanhuitz, *Nelson* 4394 (US). NAYARIT: Vicinity of Acaponeta, Tepic, *Rose* 3114 (US); *Rose et al.* 14221 (US). JALISCO: Near Chapala, *Rose & Painter* 7671 (US). Tequila, *E. Palmer* 371 in 1886 (MICH, US). Corcovado Canyon, 11 mi. NE. of Autlán, *R. L. & C. R. Wilbur* 2376 (MICH, US). Five mi. E. of Autlán, *R. L. & C. R. Wilbur* 2234 (MICH, US). QUERÉTARO: *Bro. Aguiel* 10446 (US). HIDALGO: Huejutla, *C. & E. Seler* 620 (US). VERA CRUZ: Mirador, *Wawra* 968 (W). Soledad, *Wawra* 544 (W). Barranca de Zacuapan, *Purpus* 2057 (US). SAN ANDRÉS TUXTLA: Between Los Mangos and San Juan de Azúcar, *Dressler & Jones* 206 (US). MORELOS: Yautepec, *Rose et al.* 5345 (US), 6560 (US). Cuantla and vicinity, *Pringle* 9405 (US); *Lyonnet* 673 in part (US). Xochiltepec, *Lyonnet* 2159 (US). MEXICO: *Wawra* 393 (W). TEMASCALTEPEC: Rincón del Carmen, *Hinton* 1742 (US). Tenayac, *Hinton* 4018 (US). MICHOACÁN: One mi. W. of Coahuayana, 20 mi. SE. of Tecoman, *Turner* 1973 (MICH). South shore of Lake Chapala, *Schery* 173 (MICH). ZITACUARO: Zitacuaro-Tuzantla, *Hinton* 13073 (MICH, US). HUETAMO: Tacupa, *Hinton* 5622 (US). COLIMA: Colima, *E. Palmer* 165 in 1897 (MICH, S, US). Manzanillo, *E. Palmer* 912 in 1890

(MICH, US). REVILLAGIGEDO ISLANDS: Clarion Island, *Howell* 8372 (US); *Mason* 1560 (MICH, US); *Anthony* 408 (US). Socorro Island, *Barkelew* 247 (US). GUERRERO: Agua de Correa, *Langlassé* 403 (US). Acapulco and vicinity, *E. Palmer* 193 in 1894–95 (US). Cañon de la Mano Negra, near Iguala, *Rose et al.* 9329 (US). OAXACA: Oaxaca and vicinity, *Conzatti* 1601 (US); *Rose & Hough* 4646 (US). Between Mitla and Oaxaca, *J. N. & N. S. Rose* 11285 (US). Half a km. E. of and 4 km. NNE. of Tehuantepec, *King* 320 (MICH). Puerto Angel, *Morton &* Makrinius 2641 in part (US). TUXTEPEC: Chiltepec and vicinity, *Martinez-Calderon* 265 (US). TABASCO: Reforma, Belancan, *Matuda* 3189 (MICH). CAMPECHE: Tuxpeña, *Lundell* 966 (MICH, US). YUCATÁN: San Anselmo, *Gaumer* 2208 (MICH, S, US, W). Uxmal, *Steere* 2016 (MICH). Chichen Itzá, *Steere* 1394 (MICH). Yot Tzonot, *Gaumer* 1332 (MICH).

GUATEMALA: Agua Blanca, *Tejada* 104 (US). HUEHUETENANGO: Chorulá, *C. & E. Seler* 2867 (US). ALTA VERAPAZ: Chamiquin, *von Türckheim* 560 (US, W). IZABAL: Quiriguá, *Standley* 23796 (US). ZACAPA: Gualan, *Kellerman* 5617 (US). SANTA ROSA: La Vega, *Heyde & Lux* 6079 (US).

BRITISH HONDURAS: Lower Belize River, *Record* s.n. (US). Corozal District, *Gentle* 313 (MICH), 282 (MICH), 344 (MICH). Corozal, *Lundell* 4797 (MICH). Santa Rita, *Gentle* 579 (MICH).

HONDURAS: Mosquito coast, *Wullschlägel* 56 (W). Guaymas, *Standley* 55454 (US). GRACIAS: *Hjalmasson* s.n. (S). SANTA BÁRBARA: San Pedro Sula, *Thieme* 5154 (US). MORAZÁN: Zamorano, *Molina R* 371 (US).

SALVADOR: *Renson* 12 (US). Finca San Nicolas, *Choussy* 88 (US). AHUACHAPÁN: *Padilla* 410 (US). Vicinity of Ahuachapán, *Standley* 19946 (US). SANTA ANA: *Calderón* 395 (US). SONSONATE: Santa Emilia, *Standley* 22065 (US). Armenia, *Standley* 23436 (US). LA LIBERTAD: Vicinity of Ateos, *Standley* 23380 (US). SAN SALVADOR: *Calderón* 19 (US). *Velasco* 8923 (US). Vicinity of San Salvador, *Standley* 19417 (US), 20571 (S, US). San Martin and vicinity, *Calderón* 436 (US); *Standley* 22537 (US). SAN MIGUEL: Laguna de Olomega, *Standley* 20999 (US). Hacienda Potrero Santo, S. side of Lake Olomega, *Tucker* 849 (US).

NICARAGUA: CHINANDEGA: *Baker* 581 (US). CHONTALES: *Friedrichsthal* 711 (W).

COSTA RICA: Nicoya, *Cook & Doyle* 664 (US).

BAHAMAS: NEW PROVIDENCE: *Britton & Brace* 594 (US). Near Nassau, *Curtiss* 21 (L, US). Lake Killarney, *E. G. Britton* 3285 (US).

CUBA: *Jamain* s.n. collected 1863 (W). *de la Sagra* 111 (W). *C. Wright* 3509 (US). PINAR DEL Río: Near Guanajay, *W. Palmer & Riley* 668 (US). HABANA: *Baker & Wilson* 363 (US). Vedado, *Ekman* 21 (S). MATANZAS: Yumury Valley, *Rugel* 41 (L). LAS VILLAS: Vicinity of Soledad, *Howard* 5013 (MICH, US); *Morton* 4261 (US). District Cienfuegos, *Combs* 273 (US). Limones, Soledad, Cienfuegos, *Jack* 6250 (S). Banao Mts., *Bro. León* 21940 (US). ORIENTE: Santiago de Cuba and vicinity, *E. Palmer* 375 in 1902 (US), *Ekman* 8037 (S). Vicinity of San Luis, *Pollard & W. Palmer* 331 (US). Bayate, Central Miranda, *Ekman* 5681 (S), 9662 (S). Central highway, Santa Rita, Jiguaní, *Bro. Clemente* 6073 (US).

HAITI: Vicinity of Port-au-Prince, *Leonard* 2854 (US). Vicinity of St. Marc, *Leonard* 2962 (US), 2966 (US). Vicinity of Fond Parisien, Etang Saumatre, *Leonard* 4188 (US). Vicinity of Jean Rabel, *E. C. & G. M. Leonard* 13041 (US). Miragoane, *Eyerdam* 22 (US), 170a (US), 489 (US). Massif des Matheux, Mirebalais, *Ekman* H2291 (S, US). Massif de la Selle, Petionville, *Ekman* H8113 (S, US). DU NORD: Vicinity of St. Michel de l'Atalaye, *Leonard* 7310 (US), 7352 (US). DE L'ARTIBONITE: Vicinity of Ennery, *Leonard* 8910 (US).

TORTUE ISLAND: Basse Terre, *E. C. & G. M. Leonard* 12510 (US). La Vallée, *E. C. & G. M. Leonard* 15358 (US), 15520 (US). Palmiste, *Ekman* H5123 (S). GONAVE ISLAND: Vicinity of Pikmi, *Leonard* 5130 (US).

DOMINICAN REPUBLIC: Santo Domingo, *Ritter* Jan. 1823 (W); *C. Wright et al.* 132 (US); *von Türckheim* 2502 (L, S, US); *Ekman* H12505 (S, US); *Allard* 13109 (US), 13375 (S, US), 13682 (US), 14028 (US). Santo Domingo, Azua, *Rose et al.* 4418 (US), 4003 (US). Near Constanza, *von Türckheim* 3251 (L, S, US, W). Puerto Plata, *Raunkiaer* 1103 (US), 1191 (US). Haina, *Faris* 21 (US), 30 (US), 80 (US), 156 (US). SANTIAGO: Santiago, *Raunkiaer* 903 (US). Novarrete, *Abbott* 1106 (US), 1109 (US). La Delgada, *Jiménez* 1002 (US). BARAHONA: Near Barahona, *Fuertes* 66 (L, S, US, W). SAN JUAN: Juan Santiago, *R. A. & E. S. Howard* 9222 (S, US). MONTE CRISTE: Moncion *Valeur* 183 (MICH, S, US), 849 (US).

JAMAICA: *Swartz* s.n. (S). *Cuming* 99 (W). ST. ELIZABETH: Pepper, *Harris* 9861 (US). LOWER CLARENDON: Inverness, *Harris* 12751 (US).

PUERTO RICO: *Wydler* 305 (L). Toa Alta, *Stahl* 603 b (L). Road from Guayama to Aguirre, *Underwood & Griggs* 388 (US), 412 in part (US). Aguirre, *Goll* 549 (US). Road from Coamo to Ponce, *Underwood & Griggs* 579 (MICH, US). Between Coamo and Aybonito, *Sintenis* 1971 (US). Coamo Springs, *Goll* 729 (US); *Heller* 6108 (L, US). Guaraguao, Ponce, *Goll* 818 (US). Magueyes, Ponce, *Goll* 777 (US). Along Rio Portuguese, Ponce, *Underwood & Griggs* 726 (US). Guanica, *Sargent* 30 (US); Smyth 5013 (US). Cabo-Rojo, *Sintenis* 801 (L, S, US). Between Peñuelas and Tallaboa, *Sintenis* 4817 (L). VIEQUES ISLAND: Santa Maria to Caballo Colorado, *Shafer* 2692 (US).

LESSER ANTILLES: U.S. VIRGIN ISLANDS: ST. CROIX: *West* s.n. (L). Bassin, *Ricksecker* 98 (US). Frederiksted, *Rose et al.* 3201 (US). Grange, *Oersted* s.n. (S); *Hansen* s.n. (S). Anna's Hope, *Thompson* 878 (S). BRITISH VIRGIN ISLANDS: TORTOLA: Bank, Sea Cow Bay, *Britton & Shafer* 925 (US). Experiment Station, *Fishlock* 12 (US), 163 (US). ST. BARTHÉLEMY: *von Goës* s.n. (S). *Forsström* s.n. (S). ST. EUSTATIUS: *Suringar* May 1885 (L). ST. KITTS: Near Sandy Point, *Britton & Cowell* 149 (US). ANTIGUA: Near Bellevue, *Box* 932 dupl. (US). St. John's, *Ramsammy* 110 (US). MONTSERRAT: Plymouth, *Shafer* 1 (US); *Potter* 5553 (GH). GUADELOUPE: *Duss* 2671 (US). Pointe-à-Pitre, *Hammarlund* 32 (S). Jarry, *Questel* 598 (US). Gosier, *Questel* 2472 (US). MARIE GALANTE: *Questel* 1456 (US). DOMINICA: Wallhoure, *Eggers* 652 (L). ?ST. LUCIA: ?Grande Anse, *Eggers* 6460 (US). GRENADA: *Eggers* 6460 (US). St. George, *Broadway* s.n. (US). Victoria, *Suringar* s.n. (L).

VENEZUELA: Las Adjuntas and Rio Macarao, *Eggers* 13277 (L, US; these specimens lead toward *M. pyramidata* var. *hieronymi*). MIRANDA: Around Dos Caminos and Los Chorros, *Pittier* 5923 (US). FEDERAL DISTRICT: Caracas, San Bernardino, *Fernández* 194 (US). Lower Catuche wood above Caracas, *Pittier* 7026 (US). ARAGUA: Maracay, *Vogl* 336 (S).

COLOMBIA: Plages de la Magdalena, *Goudot*, collected 1844 (P). MAGDALENA: Santa Marta, *H. H. Smith* 472 (L, S, US). ATLÁNTICO: Barranquilla and vicinity, *Bro. Elias* 1343 (US, W). Usiacurí, Arroyo Cagón, *Dugand & Garcia Barriga* 2346 (US). Between Palmar de Varela and Pondera, *Dugand* 4509 (US). Puerto Colombia, *Pennell* 12025 (US); *Dugand* 5473 (US). BOLÍVAR: Cartagena and vicinity, *Billberg* 34 (S); *Killip & Smith* 14159 (US). Sincelejo, *Pennell* 4073 (US). Turbaco, *Bro. Heriberto* 494 (US). ?TOLIMA: Tocaima, *Arbelaez* 2092 (US). HUILA: Río Cabrera ca. 18 km. NE. of Villavieja, *S. G. Smith* 1197 (US). ANTIOQUIA: Occidente, *Peláez et al.* 581 (US). VALLE DEL CAUCA: Cuchilla, E. of Zarzal, *Pennell et al.* 8529 (US). Zaragoza, *Cuatrecasas* 22782 (US). CAUCA: Cali and vicinity, *Pittier* 619 (US). Cerrito in Cauca Valley, *Lehmann* 3866 (US).

ECUADOR: GUAYAS: Guayaquil and vicinity, *Asplund* 5113 (R, US); *Fagerlind & Wibom* 105 (S); *Mille* s.n. (MICH); *Haenke* s.n. (W). Oil camp between Guayaquil and Salinas, *Hitchcock* 19983 (US). Vicinity of Durán, *J. N. & G. Rose* 23615 (US).

PERU: SAN MARTÍN: Pucayacu 11 km. from Tarapoto, *Ferreyra* 7752 (US). LORETO: Maucallacta, Río Paranapura, *Klug* 3927 (S, US).

BOLIVIA: SANTA CRUZ: Cabezas, *Peredo* 443 (UC). Cabezas Laguna del Turco, *Peredo* 146 (S).

BRAZIL: *Sellow* s.n. (US). MARANHÃO: Island of São Luiz, *Frões* 11887 (US), 24080 (US). CEARÁ: *Allemão & Cysneiros* 133 (R, US). Fortaleza to Crato, *Duarte* 1383 (US). FORTALEZA: Floresta, *Drouet* 2324 (MICH, S, US). Maracanaú, *Fernandez* 30 (R); *Ducke* 2606 (US). Ipú, *Löfgren* 213 (S). Cedro, *Löfgren* 74 (S). PARAÍBA: *Xavier* s.n. (R). Areia, *Vasconcellos* 271 (US). PERNAMBUCO: Olinda, *Bento* 40 (RB). São João dos Pombos, *Falcão et al.* 1015 (US). Tome, Recife, *Monteiro* 210 (R). BAHIA: Serra Jacobina, *Blanchet* 2677 (W). Sento Sé, *Campos Porto* 2470 (RB). MINAS GERAIS: *Glaziou* 13553 (P). Arassuahy near Rio Manso, *Glaziou* 13557 in part (R). ITUIUTABA: Funda, *Macedo* 2449 (US). GOIÁS: *Gardner* 3605 (W). Between Corallinho and Cazada Telha, *Pohl* 2801 (W). About 13–15 km. E. of Formosa, *Dawson* 15098 (US). DISTRITO FEDERAL: *Occhioni* 425 (US). MATO GROSSO: Corumbá, *Hoehne* 2983 (R), 3385 (R). Aquidauana, *Reiss* s.n. (GH). GUANABARA: Mundo Novo, Botafogo, *Kuhlmann* ?4151 (RB). Corcovado, *Diomsio* (RB). Margin of Lake Rodrigo de Freitas, *Guerra* s.n. (US). RIO DE JANEIRO: Araruama near Cabo Frio, *Glaziou* 10326 (R). SÃO PAULO: *Sellow* 5288 in part (R). PARANÁ: S. Jeronimo da Serra, *Hatschbach* 3726 (US). Procedência Cruzeiro do Oeste, Serra Dourada, Rio Iraí, *Braga & Lange* 60 (US). RIO GRANDE DO SUL: S. Borja, *Rambo* (PACA 3048). Fazenda do Jarau near Quaraí, *Rambo* (PACA 27197).

URUGUAY: Fray Bentos, *Fruchard* Feb. 11, 1877 (P, US). CERRO LARGO: Rio Negro y a: Palleros, *Rosengurtt* B2044 (US).

PARAGUAY: Upper part of River Apa, *Hassler* 8037 (S). BETWEEN RIO APA AND RIO AQUIDABAN: Centurión, *Fiebrig* 4009 (L); Caballero-cué, *Fiebrig* 4780 (L).

ARGENTINA: CORRIENTES: SAN MARTIN: La Cruz boca rios Aguapey and Uruguay, *Ibarrola* 1792 (UC). Estacion Yapeyu-costa Uruguay, *Ibarrola* 1903 (S). MONTE CASEROS: Libertad, Costa, Arroyo Curuzú, *Ibarrola* 2491 (S). PASO DE LOS LIBRES: Arroyo Yatay, *Cristóbal et al.* 17 (UC). MISIONES: Candelaria, *G. J. Schwarz* 503 (US). Loreto, *Montes* 73 B (US). Posadas, *Vattuone & Bianchi L.* 92 (US). ENTRE RIOS: Conception del Uruguay, *Lorentz* Apr. 1876 (W).

MASCARENES: RÉUNION: St. Denis, *D'Alleizette* s.n. (L). MAURITIUS: *Commerson* 456 (L). *Bojer* s.n. (W). *Andersson* s.n. (S).

SUNDA ISLANDS: JAVA: PAROEROEA: Bantoer, *Backer* 36519 (L). Road from Bantoer (to) south coast, *Backer* 3876 (L). CELEBES: Boeton, *Kjellberg* 28 (L, S); *C. B. Robinson* 2494 (US). TIMOR: Collector not given (L).

MOLUCCAS: KISAR: E. of Wonreli, inland, *Bloembergen* 3867A (L). TANIMBAR: JAMDENA: Sifnana near Saumlaki, *Pleyte* 35 (L).

NEW GUINEA: PAPUA: CENTRAL DIV.: NAKEO: Baroka, *Brass* 3753 (US).

AUSTRALIA: NORTHERN TERRITORY: 25 mi. NNE of Mt. Sanford Outstation, *Perry* 2174 (US). QUEENSLAND: *Dietrich* s.n. (US). Near Morestone Station, *Perry* 1010 (US).

This species is related to *Melochia tomentosa* L. The latter is usually a taller plant, with hairier leaves, often canescent on both surfaces.

The inflorescences of *M. tomentosa* are usually axillary, those of *M. pyramidata* are usually leaf-opposed. The fruit of *M. tomentosa* has a longer rostrum and is often supported by a longer stipe. The calyx of *M. tomentosa* is often longer (5–8.6 mm. vs. 3.7–6.2 mm. long).

The stem contains fine silky fibers (Fróes). The flowers open 8 a.m. and close 11 a.m. (Runyon).

51b. Melochia pyramidata L. var. **hieronymi** Schum. *in* Mart. Fl. Bras. 12(3):35. 1886.

Melochia pyramidata L. *Grisebachii* O. Ktze. Rev. Gen. Pl. 3(2):25. 1898.
Melochia pyramidata L. *flava* O. Ktze. Rev. Gen. Pl. 3(2):25. 1898.
Melochia pyramidata L. var. *Hieronymi* Schum. f. *follis luteo variegatis* and f. *transitoria*, both Schum. & Hassl. Bull. Herb. Boiss. II, 4:70. 1903.
Melochia tomentosa L. var. *mattogrossensis* R. E. Fries, Svensk. Vet. Akad. Handl. 42(12):10. 1908.
?*Melochia pyramidata* L. var. *paraguariensis* Hassl. f. *intermedia* Hassl. Buenos Aires Univ. Nat. Inst. Bot. y. Farm. Trab. 21:85. 1909.
?*Melochia pyramidata* L. var. *pseudotomentosa* Hassl. Repert. Nov. Sp. Fedde 8:122. 1910.

This variety is hairier than the typical variety. The upper surface of the leaf is hirsute and the lower surface is tomentulose. Often there are more flowers per umbel.

TYPE LOCALITY: Southern Brazil, Paraguay, and northern Argentina. Sellow 1751 (W) collected in Brazil, and cited below, is selected as lectotype.

DISTRIBUTION: Northern South America to northern Argentina.

VENEZUELA: FEDERAL DISTRICT: Caracas, *van Landsberge* 340 (S). Above Caracas, Middle Catuche wood, *Pittier* 9812 (US). Middle Cotiza, near Caracas, *Pittier* 7059 (GH, US). Road from country club to Rio Chacito, *Lasser* 656 (US).

COLOMBIA: NORTE DE SANTANDER: Valle del río Peralonso near Santiago, *Molina & Barkley* 18 N. S. 137 (US). SANTANDER: Near Quebrada Monte Grande 2 km. W. of Jordan, *Langenheim* 3095 (US). CUNDINAMARCA: Jerusalén, collector not given (US). TOLIMA: Valle del rio Magdalena, Armero, *Cuatrecasas* 10486 (US), 10486–B (US). VALLE DEL CAUCA: Cali Loma, *Dryander* 2200 (US). Cuchilla, E. of Zarzal, *Pennell et al.* 8529 (GH). CAUCA: Cali and vicinity, *Figueroa P.* 906 (US). La Manuelita, near Palmira, E. side of Cauca Valley, *Pittier* 791 (US).

PERU: LORETO: Tarapoto, *Ule* 6529 (L). JUNÍN: La Merced, *Macbride* 5312 (GH, US). TARMA: Between La Merced and Quimiri, Chanchamayo, *Ferreyra* 3693 (US).

BOLIVIA: SANTA CRUZ: SARA: Rio Surutú, *Steinbach* 7241 (K, S, US neg. 5420 ex K).

BRAZIL: *Sellow* 1751 (W, lectotype of the variety). PARAÍBA: Experimental Station de Alagoinha, *Deslandes* 4 (RB). GOIÁS: Fazendina in Via ad Caretao, *Pohl* 1738 (W). MATO GROSSO: Corumbá, *Malme* 3072 (S, type of *M. tomentosa* L. var. *mattogrossensis* R. E. Fries, also US neg. 5609); *Hoehne* 3010 (R, US), 3011 (R), 3012 (R); *Pereira et al.* 113 (RB). Cáceres, *Hoehne* 4335 (R). SÃO PAULO: Rio Piracicaba, *de Lima* s.n. (RB). Iporanga, margin of Rio Ribeira, *Hatschbach* 5190 (US). RIO GRANDE DO SUL: Fazenda Santa Cecilia near S. Gabriel, *Rambo* (PACA 25662), (PACA 25765).

PARAGUAY: Villa Rica, *Jorgensen* 3917 (S, US). Est. Armonia, *Anisits* 2000 (S). Cordillera de Altos, *Fiebrig* 370 (K, L). Asunción, ?*Diciers* 20 (K). Central Paraguay, *Morong* 588 (US). ALTO PARAGUAY: Chaco, 21° S. Lat., ***Fiebrig*** 1275 (S).

ARGENTINA: SALTA: Chicoana, *Zabala* 121 (GH, US). Capital, *Krapovickas* 1445 (S). Salta City, N. Caseros, *Wall & Sparre* 1187 (S). ANTILLAS: Cerro Negro, *Venturi* 10404 (S). GUACHIPAS: Alemania, *Venturi* 9914 (GH, S, US), 9971 (S, US). TUCUMÁN: Estacion agricola esperimental, *Skottsberg* s.n. (S). Camino a San Andrés, *Cuezzo* 28 (S). Tusca and Taruca Pampa at La Cruz, *Lorentz & Hieronymus* 61 (US). CAPITAL: Mataderos ?, *Venturi* 2190 (A, S), 2190 in part (US). TRANCAS: Vipos, *Venturi* 5017 (GH, US). TAFI: Tipa, *Rocha* 3656 (US). Cuesta Pariquillo, *Venturi* 2621 (US). SANTIAGO DEL ESTERO: C. PELLEGRINI: Cerro del Remate, *Venturi* 5654 (US). CHACO: *Jorgensen* 2541 (US). Fontana, *Meyer* 2309 (GH). CORRIENTES: CONCEPCION: Loma Alta, *S. Ybarrola* 1116 (US). MISIONES: Posadas, Bonpland, *Ekman* 1975 (S). CANDELARIA: Puerto Santa Ana, *G. J. Schwarz* 612 (UC). Arroyo "Martin chico," *G. J. Schwarz* 568 (UC).

Section V. *Physodium* (Presl) A. Goldberg, stat. nov.

Physodium Presl, Rel. Haenk. 2:150. 1835.

Shrubs or small trees 2–10 meters high, the young stems and petioles tomentulose, hairs yellow brown, stellate, sometimes also glandular, 0.1–0.7 mm. long, internodes 1.0–5.5 cm. long; stipules 2.5–6. 0 mm. long, 0.2–1.2 mm. wide, deltoid-acuminate, lanceolate or nearly linear, densely pubescent, hairs stellate, 0.1–0.6 mm. long; petiole 1–3.5 cm. long.

Lamina 3.5–14.8 cm. long, 2.6–11.5 cm. wide, ovate, one side usually larger than the other, the base rounded, truncate or cordate, sometimes oblique, the apex acute to acuminate, woolly or scabrous to the touch, the upper surface covered with stellate hairs 0.1–0.5 mm. long, sometimes also with resin-colored granules or pulverulent, the lower surface tomentulose, hairs stellate, 0.2–0.6 mm. long, young leaves densely covered with hairs, older leaves sometimes subglabrate, the margin irregularly crenate-serrate, serrations 1.5–7.5 mm. wide, 0.5–3.2 mm. high, 5–7 pairs of primary veins, 2 or 3 are basal.

Inflorescences terminal, extending 2–9 cm. beyond the first leaf, corymbiform, the ultimate divisions umbellate, 3–9 flowers per umbel, also axillary, 1.5–12.5 cm. long, in the axils of the upper 1–11 or more leaves, the peduncle 0.3–2.7 cm. long, with a primary branch 0.2–2.4 cm. long, a secondary one 0–1.3 cm. long, and a tertiary one 0–0.7 cm. long, the pedicel 2.5–13 mm. long at anthesis, becoming 5–19 mm. long in the fruiting stage, covered with stellate, and sometimes also glandular hairs 0.1–0.8 mm. long; bracts 1.5–6.2 (–11) mm. long, 0.2–0.7 (–1.6) mm. wide, lanceolate to nearly linear, densely covered with stellate, and sometimes also glandular hairs 0.1–0.6 mm. long.

Calyx rose, rose purple or yellow, densely pubescent, hairs stellate and sometimes also glandular, 0.1–0.8 mm. long, at anthesis 7–15 mm. long, 3.6–8.5 mm. wide, with teeth 1.7–4.5 mm. long, 1.5–3.5 mm. wide, accrescent, becoming 15–36 mm. long, 8–19 mm. wide, with teeth 3–12 mm. long, 3–10 mm. wide, the teeth deltoid-acute or deltoid-acuminate, the sinus acute, inflated calyx acutely pentagonal, reticulate-veined and with a midrib leading to each tooth and a vein to each sinus; sometimes with glandular tissue between the calyx and corolla for 0.5–1.2 mm. and 0.8–1.0 mm. high between the bases of the petals; petals red, pink, yellowish red, light blue, violet blue, violet or mauve, 8–17.4 mm. long, 2.0–9.5 mm. wide, oblanceolate, obdeltoid or obovate-oblong, spatulate, sometimes slightly emarginate at the apex, attached to the staminal tube for 2.5 mm., the claw 2.5–6.5 mm. long, somewhat thickened, with a few glandular hairs and sometimes also forked and stellate hairs, 0.1–0.7 mm. long on both surfaces; anther 1.4–2.6 mm. long, 0.6–1.2 mm. wide, oblong, slightly emarginate at both ends.

Longistylous form. Stamens 5.3–6.8 cm. long, with a few forked or stellate hairs 0.1–0.2 mm. long at the base of the staminal tube, the filaments free for 0.4–1.4 mm.; staminodes 0–0.2 mm. long; pistil 6.2–7.8 mm. long, the styles 3.5–6.0 mm. long, free to the ovary, papillose and slightly clavate at the apex for 0.7–1.0 mm., with forked, stellate, and simple hairs 0.2 mm. long, the ovary globose, pentagonal, covered with stellate or glandular hairs 0.1–0.2 mm. long, the stipe 1–4.3 mm. long.

Brevistylous form. Stamens 6.2–10.3 mm. long, sometimes with very few stellate hairs 0.1 mm. long at the base of the staminal tube, the filaments free for 1.5–5.0 mm.; staminodes 0–1.2 mm. long; pistil 3.2–6.5 mm. long, the styles free to the ovary, 0.8–5.3 mm. long, papillose for 0.3–1.0 mm. at the apex, the stipe 1–4.5 mm. long.

Fruit 5.3–7.7 mm. long, 6.7–8.8 mm. wide, globose, acutely pentagonal, slightly retuse at the apex, the sulci between the carpels rather deep, extending a third to half way to the center of the fruit, tomentulose, hairs stellate and sometimes also glandular and simple, 0.1–0.5 mm. long, the stipe 4.3–6.7 mm. long; dehiscence loculicidal all along the dorsal suture; seeds 2.8–3.9 mm. long, 1.6–2.5 mm. wide, obovate, trigonal or somewhat flattened, dark brown, 1 or 2 per cell.

Flowering specimens collected December–April, June, July, September, October; fruiting ones, December–July.

TYPE SPECIES: *Melochia corymbosa* (Presl) Meissn. ex Steud.

DISTRIBUTION: Sinaloa to Oaxaca, Mexico, in wet woods, on rocky, shady canyon slopes in the short-tree forest, on wooded, grassy hills, in shade along small streams, on hills covered with dry-season deciduous forest, at 250–1,650 meters elevation.

52. Melochia adenodes A. Goldberg, sp. nov.

Frutex vel arbor parva; laminis foliorum asymmetrice ovatis, basi rotundatis, truncatis vel cordatis, obliquis, apice acutis vel acuminatis, juvenilibus utrinque dense stellato-tomentosis; inflorescentiis terminalibus et axillaribus, corymbiformibus sed ramulis ultimis cymoso-umbellatis, pedicellis calicibusque pilis glandulosis valde vestitis; petalis 8–12 mm. longis, calycem per anthesin haud superantibus; staminodiis 0.2–1.2 mm. longis.

A shrub to small tree 2–10 meters high, bark ashy, the young stems and petioles densely covered with yellow-brown stellate hairs 0.1–0.3 mm. long, glandular hairs sometimes also present, internodes 1–4.3 cm. long; stipules soon deciduous, 2.6–3.4 mm. long, 0.5–0.6 mm. wide, lanceolate, densely covered with stellate hairs 0.1–0.3 mm. long; petiole 1–3.5 cm. long.

Lamina 4–14.8 cm. long, 2.6–11.5 cm. wide, ovate, one side of the leaf usually larger than the other, the base usually oblique, truncate, cordate or rounded, the apex acute to acuminate, young leaves densely covered with stellate hairs, 0.1–0.3 (–0.5) mm. long, sometimes also with resin-colored granules, or pulverulent on the upper surface, woolly to the touch, older leaves subglabrate, the margin irregularly crenate-serrate, serrations 1.7–7.0 mm. wide, 0.5–2.5 mm. high, 6 or 7 pairs of primary veins, 2 (–3) are basal.

Inflorescences 3–12.5 cm. long, in the axils of the upper 1–11 or more leaves, also terminal extending 3–9 cm. beyond the first leaf, corymbiform, the ultimate divisions umbellate, 3–6 flowers per umbel, the peduncle 0.6–2.8 cm. long, with a primary branch 0.2–2.4 cm. long, a secondary one 0–1.3 cm. long, and a tertiary one 0–0.7 cm. long, the pedicels 6–12 mm. long at anthesis, 10–19 mm. long in the fruiting stage, covered with glandular hairs 0.3–0.8 mm. long and stellate hairs 0.1–0.2 mm. long; bracts 1.5–3.7 mm. long, 0.2–0.5 mm. wide, lanceolate to nearly linear, acute, densely covered with stellate, and sometimes also glandular hairs 0.1–0.3 mm. long.

Calyx rose, rose purple or yellow, covered with glandular hairs 0.2–0.6 mm. long and fewer stellate hairs 0.1–0.2 mm. long, at anthesis 11.1–15 mm. long, 7.7–8.3 mm. wide, with teeth 2–4.5 mm. long, 2–3.5 mm. wide, accrescent, becoming 1.8–3.6 cm. long, 1.1–1.9 cm. wide, with teeth 5–12 mm. long, 6–10 mm. wide, the teeth deltoid-acute or deltoid-acuminate, the sinus acute, inflated calyx acutely pentagonal, reticulate-veined and with a midrib leading to each tooth and a vein to each sinus; internode between the calyx and the corolla 0.7–1.2 mm. long; petals pink, red, yellowish red, or pinkish orange, 8–12 mm. long, 2–2.7 mm. wide, oblanceolate or obovate-oblong, spatulate, attached to the staminal tube for 2.5 mm., the claw 2.5–6.5 mm. long, thickened, a few glandular hairs 0.1–0.2 mm. long, and

sometimes also fewer stellate hairs 0.1 mm. long, scattered over both surfaces of the petal.

Longistylous form. Stamens 6.8 mm. long, the filaments free for 1.3 mm., the anther 1.7–1.8 mm. long, 1.1 mm. wide, oblong, slightly emarginate at both ends; staminodes extending 0.2 mm. beyond the staminal tube; pistil 7.5–7.8 mm. long, the styles 6 mm. long, free to the ovary, papillose and slightly clavate for 1 mm. at the apex, scattered simple and forked hairs 0.2 mm. long all along the styles, the ovary globose, covered with glandular hairs 0.1 mm. long, the stipe 4.3 mm. long.

Brevistylous form. Stamens 6.2–10.3 mm. long, the filaments free for 1.5–5.0 mm., very few stellate hairs 0.1 mm. long at the base of the staminal tube, the anther 2–2.6 mm. long, 1–1.2 mm. wide, oblong, emarginate at both ends, more so at the base; staminodes extending 0.2–1.2 mm. above the staminal tube; pistil 3.2–6.5 mm. long, the styles 1.5–5.3 mm. long, free to the ovary, papillose and slightly clavate for 0.3–1.0 mm., the ovary globose, densely covered with glandular hairs, and sometimes also stellate hairs, less than 0.1 mm. long, the stipe 2.7–4.5 mm. long.

Fruit 6.3–7.7 mm. long, 7.5–8.0 mm. wide, globose, rather acutely pentagonal, slightly retuse at the apex, the sulci between the carpels fairly deep, extending half way to the center of the fruit, covered with stellate, glandular and simple hairs 0.1–0.3 mm. long, the stipe 6–6.7 mm. long; dehiscence loculicidal all along the dorsal suture; seeds 3–3.7 mm. long, 1.7–2.1 mm. wide, obovate, somewhat flattened, brown.

Flowering specimens collected from December to April (dry season); fruiting ones, from December to June.

Key to Varieties of *M. adenodes*

1. Calyx teeth acute, typically 5–6 mm. long in the fruiting stage.
52a. M. adenodes var. **adenodes**
1. Calyx teeth acuminate, typically 11–12 mm. long in the fruiting stage.
52b. M. adenodes var. **acuminata**

52a. Melochia adenodes A. Goldberg var. **adenodes**

The calyx is rose to rose purple, and the teeth are acute and typically 5–6 mm. long in the fruiting state. The petals are rose to red.

Type locality: The type was collected by G. B. Hinton, no. 16203, at Huizontla, Coalcoman, Michoacán, Mexico, and is cited below.

Distribution: Jalisco to Oaxaca, Mexico, in woods, in shade along small streams, on wooded grassy hills, on hills covered with dry-season deciduous forest, at 200–1,500 meters elevation.

MEXICO: S. Carlos, *Liebmann* 5888? (US). JALISCO: San Sebastian and vicinity, *Nelson* 4120 (US); *Mexia* 1485–a (MICH, US). Santa Cruz de Vallarta, *Mexia* 1289 (US). Toward La Resolana 16 mi. SSW. of Autlán, *R. L. & C. R. Wilbur* 1451 (MICH, US). Southwest of Autlán, toward Manzanillo, *McVaugh* 10231 (MICH, US). Along road from Barra de Navidad to Tequezquitlán, Concepción, and Autlán, *McVaugh* 11870 (MICH, US). MICHOACÁN: COALCOMAN: *Hinton* 12957 (US). Huizontla, *Hinton* 16203 (US, type). Aquila, *Hinton* 15815 (MICH, US). COLIMA: Manzanillo, *E. Palmer* 1372 in 1891 (MICH, US). GUERRERO: El Naranjo, *Nelson* 6987 (US). OAXACA: San Bartolo Yauhtepec, *C. & E. Seler* 1653 (US). TEQUILA: vicinity of Tuchahengo?, *Conzatti* 4552 (US).

This species has been misinterpreted by Standley (52) and others as *Physodium corymbosum* Presl. I have seen the type of the latter species. The calyx and pedicels do not have glandular hairs, those of *M. adenodes* are covered with glandular hairs. In his description Presl did not mention staminodes and his illustration did not show any, nor did I see any in the withered flower parts of the type, which is in the fruiting stage. Staminodes are quite evident in *M. adenodes*.

52b. Melochia adenodes A. Goldberg var. **acuminata** (Rose) A. Goldberg, comb. nov.

Physodium corymbosum Presl var. *acuminata* Rose, Contr. U.S. Nat. Herb. 1:309. 1895.

The calyx may be red or yellow and the teeth are acuminate and typically 11–12 mm. long in the fruiting stage. The petals are red or yellowish red to pinkish orange.

TYPE LOCALITY: Jalisco, Mexico. The type, cited below, was collected by E. Palmer, no. 86, in 1886.

DISTRIBUTION: Sinaloa to Mexico, Mexico, on rocky, shady canyon slopes in the short-tree forest, and on hills, at 280–750 meters elevation.

MEXICO: SINALOA: *Ortega* 5104 (US). Mazatlán, *Ortega* 5608 (US). Cerro Prieto, Pueblo de Coyotitan, *Montes & Salazar* 120 (US). Near Bacubirito, *W. Palmer* 1249 (US). BADIARGUATO: Arroyo de Carrisal, *Gentry* 5800 (MICH). Cerro Colorado, *Gentry* 5483 (MICH). DURANGO: Sianori, *Ortega* 5396 (US). JALISCO: Barranca of Guadalajara, *Pringle* 5882 (US); *E. Palmer* 86 in 1886 (MICH, US, type). Between La Venta de Nochitiltic and Barranquitas along Tepic-Guadalajara highway, *McVaugh* 12045 (MICH, US). MEXICO: TEMASCALTEPEC: Palmar, *Hinton* 7294 (US). MICHOACÁN: Monte de Loreto near Inguarán, *Langlassé* 17 (US).

53. Melochia rhodocalyx C. Koch & Bouché, Index Sem. Hort. Berl. 14. 1854.

PLATE 9

Physodium dubium Hemsl. Diag. Pl. Nov. 1:4. 1878.

A shrub to small tree 2–6 meters high, the young stems and petioles woolly, densely covered with yellow-brown stellate hairs 0.3–0.7 mm. long, internodes 1.5–5.5 cm. long; stipules 2.5–6.0 mm. long, 0.2–1.2 mm. wide, deltoid-acuminate to nearly linear, rather densely covered with stellate hairs up to 0.6 mm. long; petiole 1–3.5 cm. long.

Lamina 3.5–12.5 cm. long, 3.2–10.0 cm. wide, ovate, often slightly

oblique, the base rounded, truncate or cordate, woolly to the touch, hairs stellate, 0.2–0.5 mm. long, usually not overlapping on the upper surface, usually overlapping on the lower surface, the margin irregularly crenate-serrate, serrations 1.5–7.5 mm. wide, 0.5–3.2 mm. high, 5–7 pairs of primary veins, 2 (–3) basal, second basal pair extending about half way up the lamina.

Inflorescences terminal, extending 2–6.5 cm. beyond the first leaf, and axillary, 2–4 cm. long, in the axils of the upper 1–2 leaves, corymbiform, the ultimate divisions umbellate, 3–9 flowers per umbel, the peduncle 0.3–2.7 cm. long, with a primary branch 0.3–2.0 cm. long, and a secondary one 0.3–1.2 cm. long, the pedicels 5–13 mm. long at anthesis, becoming 8–15 mm. long in the fruiting stage, covered with stellate hairs 0.5 mm. long; bracts 3.2–6.2 mm. long, 0.2–0.7 mm. wide, lanceolate to nearly linear, densely covered with stellate hairs up to 0.6 mm. long.

Calyx rose, densely covered with stellate hairs 0.2–0.5 mm. long, at anthesis 10–13.3 mm. long, 6.2–8.5 mm. wide, with teeth 2.2–3.7 mm. long, 2.3–3.0 mm. wide, accrescent, becoming 1.5–2.3 cm. long, 1–1.4 cm. wide, with teeth 5 mm. long, 3 mm. wide, the teeth deltoid-acute to deltoid-subacuminate, the sinus acute, inflated calyx acutely pentagonal, reticulate-veined and with a midrib leading to each tooth and a vein to each sinus; glandular tissue extending for 0.5 mm. between the calyx and corolla and 0.8–1.0 mm. high between the bases of the petals; petals light blue, red, mauve or violet, 16–17.4 mm. long, 5.6–9.5 mm. wide, obdeltoid-spatulate, slightly emarginate at the apex, the claw 2.5–4.0 mm. long, somewhat thickened, a few simple, forked, and stellate hairs 0.1–0.2 mm. long on the abaxial surface near the base, scattered glandular hairs 0.1 mm. long on the adaxial surface.

Longistylous form. Stamens 5.3–6.8 mm. long, the filaments free for 1.0–1.4 mm., a few forked hairs 0.2 mm. long at the base of the staminal tube, staminodes none, or rarely extending 0.1 mm. beyond the staminal tube, the anther 1.6–1.8 mm. long, 0.7–1.0 mm. wide, oblong, slightly emarginate at both ends, slightly more so at the base; pistil 6.2–6.7 mm. long, the styles 4.0–5.5 mm. long, free to the ovary, papillose and slightly clavate for 0.7–1.0 mm. at the apex, forked and stellate hairs 0.2 mm. long at the base of the styles, the ovary globose, pentagonal, covered with stellate hairs 0.1–0.2 mm. long, the stipe 2.8–3 mm. long.

Brevistylous form. Stamens 8.3–8.5 mm. long, the filaments free for 3.4–3.7 mm., the anther 1.6–1.9 mm. long, 0.7–0.8 mm. wide, oblong, slightly narrower at the apex, emarginate at both ends or only at the base, more so at the base, no hairs on the androecium, staminodes none, or rarely extending 0.1 mm. above the staminal

tube, dentiform; pistil 3.5 mm. long, the styles 0.8–1.0 mm. long, free to the ovary, the ovary densely covered with stellate hairs 0.2 mm. long, the stipe 2.5 mm. long.

Fruit 6.4–7.5 mm. long, 6.8–8.8 mm. wide, globose, rather acutely pentagonal, slightly retuse at the apex, the sulci between the carpels fairly deep, extending half way to the center of the fruit, covered with stellate hairs 0.1–0.4 mm. long, the stipe 5 mm. long; dehiscence loculicidal along the dorsal suture; seeds trigonal, or somewhat flattened, 2.8–3.9 mm. long, 1.6–2.5 mm. wide, brown.

Flowering specimens collected in June, July, September and October; fruiting ones, in June and July.

TYPE LOCALITY: The species was described in 1854 from specimens grown in the Berlin Botanical Garden. The native locality was unknown to the authors. A specimen, cited below, labeled *Melochia rhodocalyx* was received by the Riksmuseum, Stockholm, Sweden, from the Berlin Botanical Garden in the above year. It may be an isotype.

DISTRIBUTION: Mexico to Oaxaca, Mexico, in wet woods, on lava beds, at the edge of a stream, on clay soil, at 1,200–1,650 m ters elevation.

Cultivated in the Berlin Botanical Garden *Andersson* s.n. (S, ?isotype, also US neg. 5610).

MEXICO: MORELOS: Near Cuernavaca, *Rose & Painter* 6949 (US); *Pringle* 6335 (MICH, S, US, W). Xochiltepec, *Lyonnet* 2164 (US); *Lyonnet & Elcoro* 1136 (US). Yautepec, *Rose et al.* 8548 (US). Xochicalco, *Kenoyer* July 18, 1938 (MICH). MEXICO: TEMASCALTEPEC: Acatitlán, *Hinton* 4338 (S, US). GUERRERO: Limon Mt., *Rusby* 18 (US). Campo Morado, Mina, *Hinton et al.* 14472 (US). El Ocote, probably near Chapultepec according to McVaugh (40), *Langlassé* 1046 (US). OAXACA: Jayacatlan, *L. C. Smith* 14 (US). Six miles above Dominguillo, *Nelson* 1847 (US).

Hemsley (25) stated, "*Physodium* does not appear to differ generically from *Melochia;* but I have followed Bentham and Hooker in referring this plant to Presl's genus." Hemsley used Andrieux no. 507 (K), collected between Acatlán and Chila, Puebla, Mexico, as the type.

Schumann (48) considered *Physodium* Presl to be a synonym of *Melochia* L.

The petals of this species exceed the calyx in length at anthesis, those of *M. adenodes* A. Goldberg do not. The petals of *M. corymbosa* (Presl) Meissn. ex Steud. are considerably shorter than those of *M. rhodocalyx.*

54. Melochia corymbosa (Presl) Meissn. ex Steud. Nom. Bot. II, 2:123. 1841.
Physodium corymbosum Presl, Rel. Haenk. 2:150, pl. 72. 1835.

A sparsely branched frutex to small tree 4.5–6.0 meters high, the

young stems and petioles tomentulose, hairs yellowish brown, stellate, 0.2–0.6 mm. long, internodes 1.5–3.5 cm. long; stipules 4 mm. long, 0.7 mm. wide, deltoid-acuminate, densely pubescent, hairs stellate, 0.3 mm. long; petiole 1–2 cm. long.

Lamina 4.8–9.0 cm. long, 3.3–7.0 cm. wide, broadly ovate, oblique, the base rounded to subcordate, the apex acute to acuminate, scabrous or woolly to the touch, the upper surface greenish, covered with stellate hairs 0.2–0.5 mm. long, the lower surface lighter green, tomentulose, hairs stellate, 0.3–0.6 mm. long, the margin irregularly crenate-serrate, serrations 1–6 mm. wide, 0.5–2.3 mm. high, 5–7 pairs of primary veins, 2 or 3 are basal.

Inflorescences terminal, extending 2.5–5.5 cm. beyond the first leaf, corymbiform, the ultimate divisions umbellate, about 5 flowers per umbel, sometimes also axillary, 1.5 cm. long, the peduncle 1 cm. long with a primary branch 0.8–1.3 cm. long, a secondary one 0.4 cm. long, and sometimes a tertiary one 0.2 cm. long, the pedicel 2.5–3.5 mm. long, becoming 5–13 mm. long in the fruiting stage; bracts deciduous, 4.5 mm. long, 0.4 mm. wide, nearly linear, with stellate hairs 0.2–0.3 mm. long.

Calyx 7 mm. long, 3.6 mm. wide, the teeth 1.7–1.8 mm. long, 1.5 mm. wide, deltoid-acute, accrescent, becoming membranous, acutely pentagonal, 1.7–2.3 cm. long, 0.8–1.6 cm. wide, the teeth 3–5 mm. long, 5 mm. wide, densely pubescent, hairs stellate, 0.1–0.8 mm. long, the sinus acute; petals 9.7 mm. long, 2.1 mm. wide, oblanceolate, with scattered glandular hairs 0.1 mm. long on the axial surface and a line of stellate hairs 0.2–0.7 mm. long on the midrib, or a few simple hairs at the base, of the abaxial surface, the claw 2.5 mm. long.

Longistylous form. Stamens 5.7 mm. long, the filaments free for 0.4 mm., staminodes none, the anther 1.4 mm. long, 0.6 mm. wide; pistil developed to fruiting stage, the styles 3.5 mm. long, free to the ovary.

Brevistylous form. Stamens 7 mm. long, the filaments free for 3.5–4.0 mm., the anther 1.7–1.9 mm. long, 0.7–0.8 mm. wide; pistil 3.2 mm. long, the styles 1.3 mm. long, free to the ovary, papillose for 0.6 mm. at the apex, the ovary densely covered with stellate hairs 0.2 mm. long, the stipe 1 mm. long.

Fruit 5.3–7.2 mm. long, 6.7–9.0 (–10) mm. wide, globose, acutely pentagonal, the angles without points, the apex retuse, the sulci between the carpels extending a third to half way to the center of the fruit, tomentulose, hairs stellate, 0.3-0.5 mm. long, the stipe 4.3–6.0 mm. long; dehiscence loculicidal along the dorsal suture; seeds 3–3.7 mm. long, 1.6–2.4 mm. wide, dark brown, 1 or 2 per cell.

Flowering and fruiting specimens collected in July.

TYPE LOCALITY: The type, cited below, was collected by Haenke in western Mexico.

DISTRIBUTION: "Western Mexico" and Oaxaca, Mexico, at 750 meters elevation.

MEXICO: "Western Mexico," *Haenke* (PR 174400a, b, c, d, type and also US neg. 5554); ?*Haenke* (W). OAXACA: Tomellin Canyon, *Pringle* 4751 (S, US).

This species differs from *Melochia adenodes* A. Goldberg in the absence of glandular hairs on the calyx and pedicels, and in the absence of staminodes. It differs from *Melochia rhodocalyx* C. Koch & Bouché in having considerably smaller petals.

New Taxa, New Names, and New Combinations

Melochia L., section *Physodium* (Presl) A. Goldberg, comb. et stat. nov.
Melochia L., section *Pyramis* A. Goldberg, nom. nov.
Melochia adenodes A. Goldberg, sp. nov.
Melochia adenodes A. Goldberg var. *acuminata* (Rose) A. Goldberg, comb. nov.
Melochia chamaedrys St.-Hil. var. *decumbens* (R. E. Fries) A. Goldberg, comb. et stat. nov.
Melochia thymifolia (Presl) A. Goldberg, comb. nov.
Melochia tomentosa L. var. *speciosa* (S. Wats.) A. Goldberg, comb. et stat. nov.
Melochia villosa (Mill.) Fawc. & Rendle var. *regnellii* (Schum.) A. Goldberg, comb. nov.
Melochia villosa (Mill.) Fawc. & Rendle var. *tomentosa* (Schum.) A. Goldberg, comb. nov.
Melochia werdermannii A. Goldberg, sp. nov.

Excluded and Doubtful Taxa

Altheria Madagascariensis DC. Prodr. 1:493. 1824.
The description is inadequate for a determination.

Antiphylla serrata Rafin. New Fl. Amer. 4:16. 1836.
Antiphylla Rafin. is attributed to *Melochia* in Index Kewensis (30) and by Dalla Torre & Harms (7), but it probably belongs to the Capparidaceae or Cruciferae.

Melochia acutangula Span. *in* Linnaea 15:174. 1841.
The description is inadequate for a determination.

Melochia Berteriana Balb. ex DC. Prodr. 1:492. 1824, is a *Waltheria* according to Index Kewensis (30).

Melochia Borbonica Cav. Diss. 6:321. 1788.
The illustration is very reminiscent of *Melochia nodiflora*, but the description does not correspond to that species.

Melochia capitata, Index Kewensis (30), erroneously attributed to Boj. Hort. Maurit. 38. 1837.

Melochia corymbosa (DC.) Hemsl. Biol. Centr. Amer. Bot. 1:130. 1879=*Riedleia corymbosa* [Moc. & Sessé] ex DC., which see.

Melochia depressa L. Sp. Pl. 674. 1753.
I have examined a microfiche photograph, taken by the International Documentation Centre, of a specimen in the Linnaean Herbarium so labeled by Solander. The specimen appears to belong to the Malvaceae.

Melochia hirsuta Turcz. Bull. Soc. Nat. Mosc. 36(1):570. 1863.
The description is inadequate for a determination.

Melochia hispida Hook. & Arn. Bot. Beech. Voy. 60. 1841.
The description is inadequate for a determination and the type cannot be located.

Melochia mollissima Desf. Tabl. ed. I, 148. 1804, nomem nudum; Pers. Syn. 2:218. 1807.
A small fragment ex P so labeled belongs to the Malvaceae. The description in Persoon is inadequate for a determination.

Melochia nipensis Britt. Mem. Torr. Bot. Cl. 16:81. 1920, is a *Waltheria*.

Melochia ovata Desf. Tabl. ed. II, 172. 1815=*Melhania abyssinica* according to Index Kewensis (30).

Melochia peruviana Desr. *in* Lam. Encyc. 4:83. 1797, based on *Melochia depressa* L. *in* Cav. Diss. 6:320, pl. 173, fig. 1. 1788, appears to be close to *Melochia chamaedrys* St.-Hil., but unlike the latter, it has only one flower per leaf axil and the leaves are tomentose.

Melochia pulverulenta Miers, Proc. Roy. Hort. Soc. 4:185. 1865.
The description is inadequate for a determination.

Melochia rotundifolia Sessé & Moc. Pl. N. Hispan. 1:106. 1889, is a *Pterostemon*.

Melochia trigyna L. ex Jackson, Index Linn. Herb. 103. 1912, nomen nudum.

Melochia truncata Wall. Cat. No. 1196 K. 1929, is a *Sida* according to Index Kewensis (30).

Melochia truncata Willd. Sp. Pl. 3:601. 1801=*Melochia corchorifolia* L. according to Index Kewensis (30), but the obcordate, cuneate lamina, monopetalous corolla, 10 stamens, and reticulate seeds of the description are not *M. corchorifolia* characters.

Melochia varronifolia Desf. Cat. Hort. Par. III, 252. 1829, nomen nudum.

Physocodon brachybotrys Turcz. Bull. Soc. Nat. Mosc. 31(1):213. 1858.
The description is inadequate for a determination.

Riddelia antiphylla Rafin. New Fl. Amer. 4:16. 1836, is attributed to *Melochia hirsuta* Cav. *in* Index Kewensis (30), but the fruit is too long to be that of a *Melochia* and the seeds differ in shape from those of *Melochia*.

Riedleia Berteriana DC. Prodr. 1:492. 1824, is a *Waltheria* according to Index Kewensis (30).

Riedleia Borbonica (Cav.) DC. Prodr. 1:491. 1824=*Melochia Borbonica* Cav.

Riedleia capitata Boj. Hort. Maurit. 38. 1837, nomen nudum.

Riedleia corymbosa [Moc. & Sessé] ex DC. Prodr. 1:491. 1824.
The description is inadequate for a determination. The petals are stated to be twice the size of those of *Riedleia odorata* (L.f.) DC. Prodr. 1:491. 1824. Very few species of *Melochia* have petals that large.

Riedleia depressa (L.) DC. Prodr. 1:491. 1824=*Melochia depressa* L.

Riedleia eriantha DC. Prodr. 1:492. 1824, belongs to the Malvaceae according to Schumann (47).

Riedleia odorata DC. Prodr. 1:491. 1824=*Melochia odorata* L.f. and *Melochia umbellata* (Houtt.) Stapf.

Riedleia Peruviana (Desr. in Lam.) DC. Prodr. 1:491. 1824=*Melochia peruviana* Desr. in Lam.

Riedleia setulosa Miq. Hoev. & De Vriese Tijdschr. 10:80. 1843 probably is a *Sida*.

Riedleia truncata (Willd.) DC. Prodr. 1:491. 1824=*Melochia corchorifolia* L. according to Index Kewensis (30), but De Candolle stated that the flower is solitary and pedunculate whereas *M. corchorifolia* has a capitate inflorescence.

Riedleja hyptoides Turcz. Bull. Soc. Nat. Mosc. 31(1):210. 1858.
The description is inadequate for a determination.

Riedleja pteronema Turcz. Bull. Soc. Nat. Mosc. 31(1):208. 1858.
The description is inadequate for a determination.

Riedleja ramosissima Turcz. Bull. Soc. Nat. Moscow 36(1):571. 1863.
The description is inadequate for a determination.

Riedleja siphonandra Turcz. Bull. Soc. Nat. Mosc. 31(1):208. 1858.
The description is inadequate for a determination.

Turnera paniculata Willd. *in* Schultes Syst. Veg. 6:678. 1820=*Melochia graminifolia* St.-Hil., according to Schumann (47), but the description in Schultes is inadequate for a determination.

Visenia Berteriana (DC.) Spreng. Syst. 3:30. 1826, is a *Waltheria* according to Index Kewensis (30).

Visenia corymbosa (DC.) Spreng. Syst. 3:29. 1826=*Riedleia corymbosa* [Moc. & Sessé] ex DC.

Visenia depressa (L.) Spreng. Syst. 3:30. 1826=*Melochia depressa* L.

Visenia ferruginea Colla, Herb. Pedem. 1:432. 1833.
I have seen two specimens from the Colla Herbarium in a folder marked *Visenia ferruginea* with descriptions on the specimen sheets which could be interpreted as corresponding to the species description of *V. ferruginea*. One is a *Waltheria* and the other belongs to the Turneraceae.

Visenia madagascarensis Spreng. Syst. 3:30. 1826.
The description is inadequate for a determination.

Visenia scabra Colla, Herb. Pedem. 1:431. 1833.
The description is inadequate for a determination.

Visenia spicata Colla, Herb. Pedem. 1:431. 1833, belongs to the Malvaceae.

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Melochia gardneri Sprague. *Gardner* 3608 (P, isotype).

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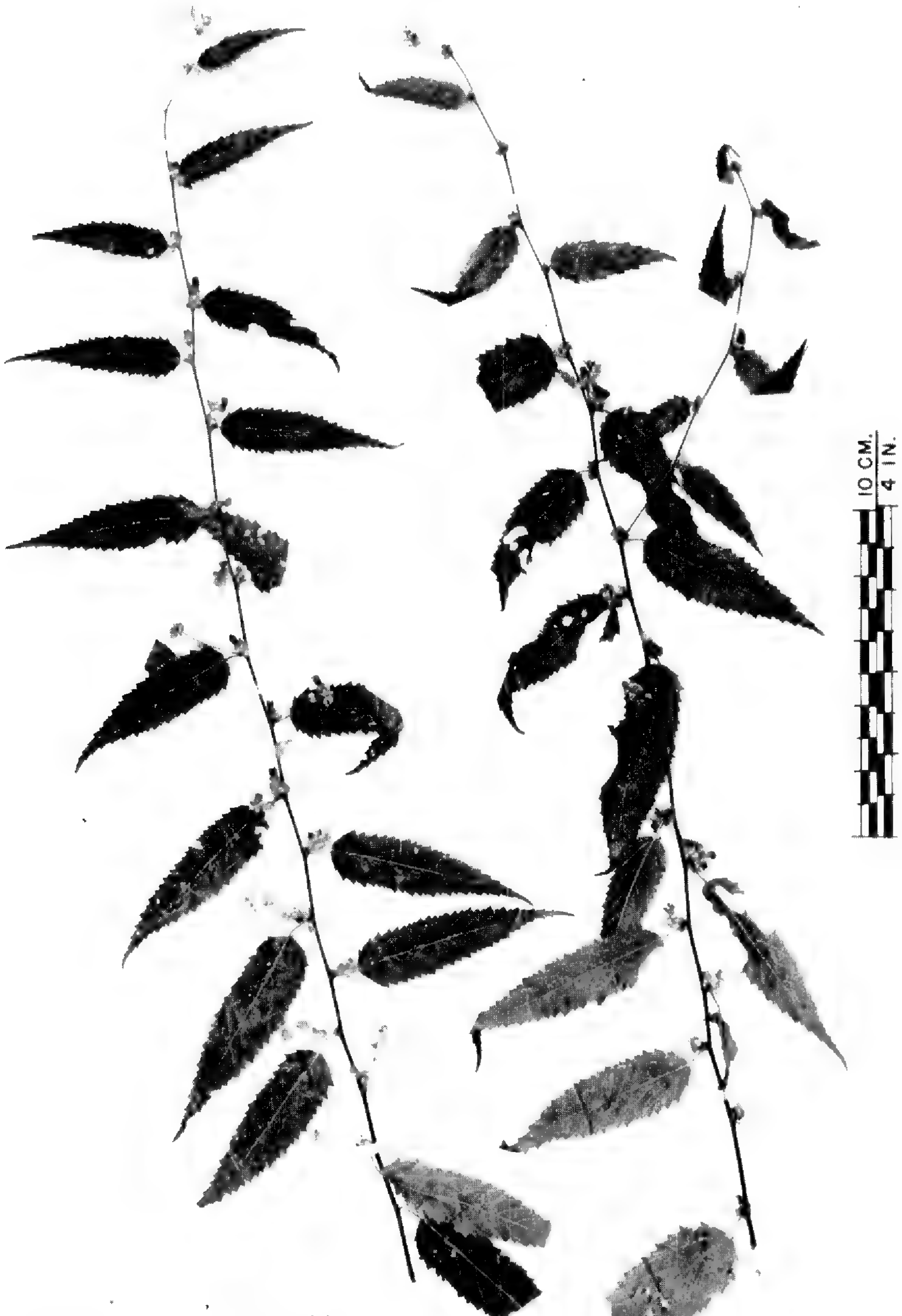
UNIVERSITY OF CALIFORNIA
Second Botanical Garden Expedition to the Andes, 1938-39

Melochia leucantha Macbride. *Stork & Horton* 10908 (UC, type).

TYPUS

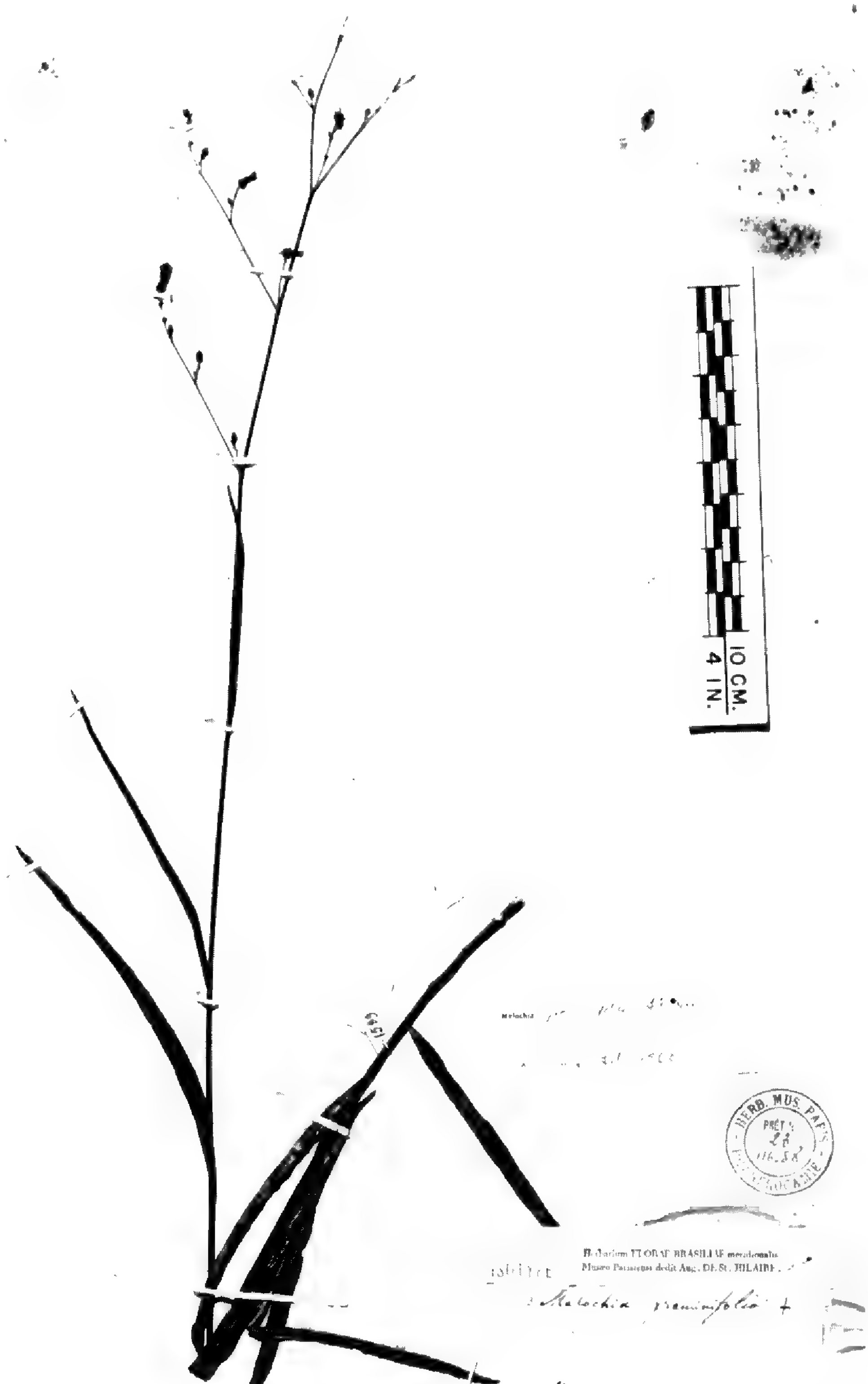
Melochia thymifolia (Presl) A. Goldberg. *Haenke* (PR 174403 a, lectotype)



TYPUS

Melochia tomentella (Presl) Hemsl. *Haenke* (PR 174404 e, isotype).

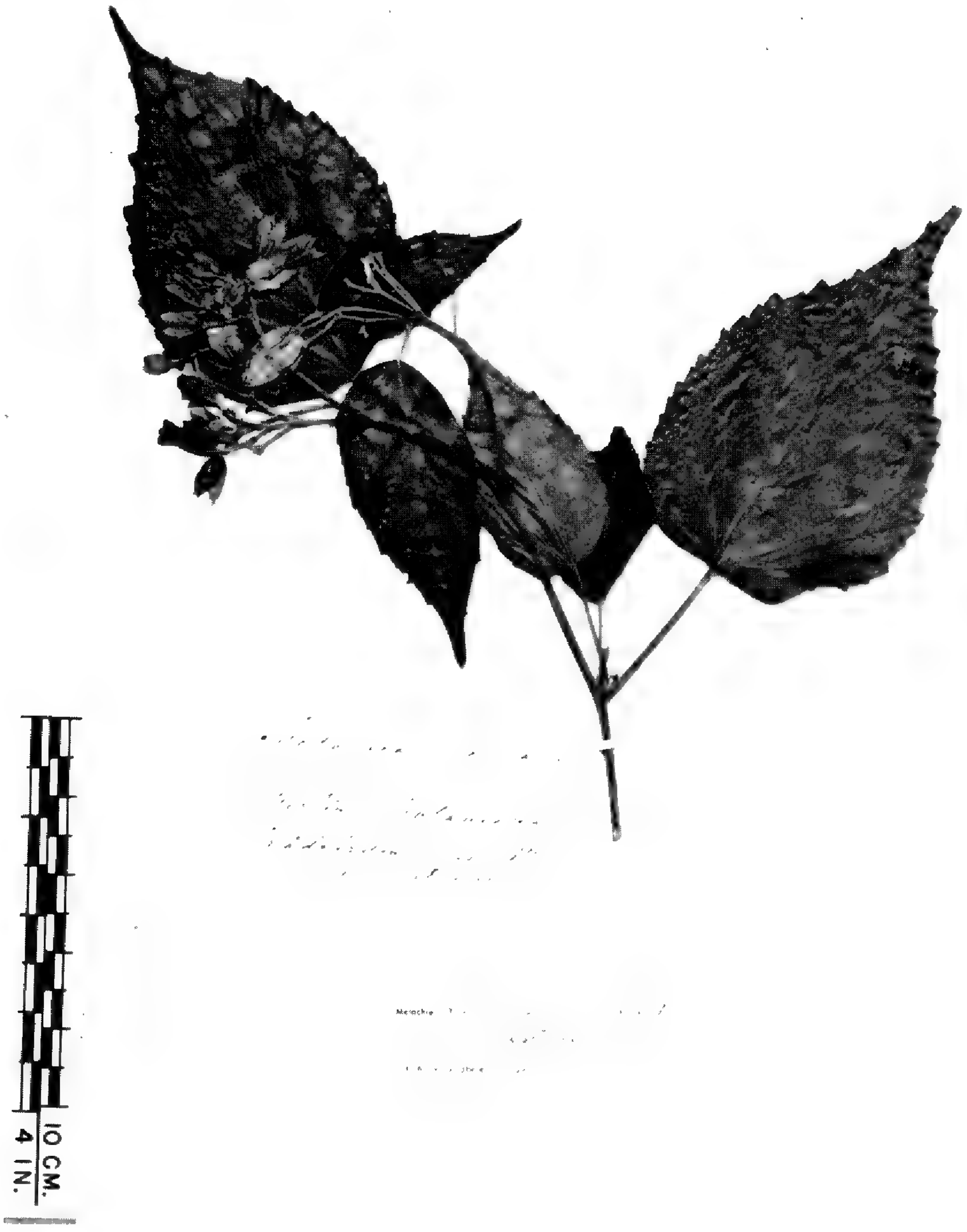
Melochia villosa (Mill.) Fawc. & Rendle. Apical portion of flowering plant, approximately twice natural size.



Melochia graminifolia St.-Hil. *St.-Hilaire* 1589 (P, isotype).

Melochia anomala Griseb. *Lorentz* 503 (GOET, type).

Melochia werdermannii A. Goldberg. *Werdermann* 2006 (S. type).



Melochia rhodocalyx C. Koch & Bouché. *Andersson* s.n. (S, perhaps isotype).

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VOLUME 34, PART 6

MEXICAN "CACALIOID" GENERA ALLIED TO SENECIO (COMPOSITAE)

By RICHARD W. PIPPEN

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MEXICAN "CACALIOID" GENERA ALLIED TO *SENECIO* (COMPOSITAE) [1]

By Richard W. Pippen [2]

Introduction

This paper represents an investigation of a geographically distinct group of North American species of Compositae occurring mainly in the highlands of Mexico. In the past these species have been considered part of the genera *Cacalia* (DeCandolle, 1838; Gray, 1883; Greenman, 1902), *Senecio* (Schultz 1845; Bentham & Hooker, 1873; Hemsley, 1881), and several distinct, smaller genera (Rydberg, 1924; Belcher, 1956; Cuatrecasas, 1960). In my study I worked out a taxonomic system for these species, then compared the species individually and as a group with superficially similar species of *Senecio*, and considered their relationships. It is now apparent that these species are generically distinct from *Senecio*, from the species in eastern North America and Asia usually referred to *Cacalia*, and also from the type-species of *Cacalia*; instead, four separate genera are represented—*Digitacalia*, *Odontotrichum*, *Pericalia*, and *Psacalium*.

The materials used in this study consisted primarily of specimens obtained from the following herbaria: Field Museum of Natural History, Chicago; Gray Herbarium of Harvard University, Cambridge, Massachusetts; Botanische Staatssammlung, München; University of Michigan, Ann Arbor; New York Botanical Garden, New York; University of Texas, Austin; and United States National Herbarium, Smithsonian Institution. I wish to express my gratitude to the curators of these herbaria who made these specimens available. Abbreviations of herbarium names used hereafter are those of Lanjouw and Stafleu (1964). The abbreviation "Field Mus. Neg." refers to Field Museum of Natural History negatives of a series of type photographs taken in European herbaria by J. F. Macbride during the period 1929 to 1939. "U. of MICH. Neg." refers to a collection of negatives of type specimens maintained at the University of Michigan Herbarium.

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[1] Part of a dissertation presented to the Horace H. Rackham School of Graduate Studies, the University of Michigan, in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

[2] Department of Biology, Western Michigan University.

Observations were made in the field, and preserved cytological materials and dried specimens were obtained during two seasons of field work in Mexico (in the summer and autumn of 1958, and the autumn of 1960), and from a survey trip through the southeastern United States in the summer of 1962.[3] Observations were also made of living plants grown from seeds and rootstocks in the University of Michigan Botanical Gardens.

All measurements were obtained from dried specimens. But flowering material of all the species was studied both in the dry state and after soaking, the latter state inducing no significant change in size. Dimensions of the heads include from the base of the phyllaries to the tip of the syngenesious anthers.

The chromosome counts were obtained by the standard aceto-carmine squash technique on pollen spore mother cells killed and fixed in Newcomer's solution. Except for *Odontotrichum decompositum* the chromosome numbers herein reported are new reports. Table 1 summarizes this information. Voucher specimens for these counts are listed in table 1 and also indicated with an asterisk (*) in the list of specimens examined under the species. Voucher specimens are preserved in the University of Michigan Herbarium.

For advice and assistance my sincere thanks and appreciation are extended to Dr. Rogers McVaugh, who initially called my attention to this problem and who collected specimens and cytological material for me on several occasions; to Dr. B. L. Turner, the University of Texas, for permitting me to cite unpublished chromosome counts from his cytological investigations of the Mexican composites; to the late Mr. N. Y. Sandwith, the Royal Botanic Gardens, Kew, who sent me special information regarding the type of *Cacalia cirsiifolia* Hook. & Arn.; to Dr. A. G. Norman, formerly Director of the University of Michigan Botanical Gardens, for the use of the facilities there for growing living plants; to Mr. J. R. Millar, formerly Chief Curator of the Herbarium, Field Museum of Natural History, for making available the botanical collections of Sessé and Mociño (then on loan to Chicago from Madrid); and to Dr. Charles Feddema, U.S. Forest Service Herbarium, for the line drawings of flower types.

Morphological Considerations

Although these species, previously referred to *Cacalia*, do apparently represent several genera, they have in common a number of morphological features and generalizations regarding these may be made. Except for *Digitacalia* (here described as new) all the genera in the

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[3] Made possible by a grant from the Graduate Student Research fund of the Horace H. Rackham School of Graduate Studies, the University of Michigan.

TABLE 1.—*Meiotic chromosome counts of some species of Mexican cacalioids*

Species	Voucher Specimens [1]	Number
Digitacalia tridactylitis	McVaugh 21903	[3] 30
Odontotrichum amplum	Pippen 4	[2] 30
Odontotrichum brachycomum	McVaugh 21934	[3] 30
Odontotrichum cirsiifolium	Pippen 52	[2] 30
Odontotrichum decompositum	–	[4] 30
Odontotrichum multilobum	Pippen 30	[2] 30
Odontotrichum palmeri	Pippen 12	ca. [2] 25
Odontotrichum pringlei	Pippen 37	[2] 30
	McVaugh 21765	[3] 30
Odontotrichum sinuatum	Pippen 9	[3] 30
Pericalia michoacana	Pippen 63, 65	[2] 30
Pericalia sessilifolia	Pippen 61	[2] 30
Psacalium eriocarpum	Pippen 62	[2] 30
Psacalium holwayana	McVaugh 21953	[3] 30
Psacalium megaphyllum	Pippen 8	[3] 30
Psacalium peltatum v. *peltatum*	Pippen 49	[2] 30
Psacalium species	McVaugh 21913	[3] 30

[1] Voucher specimens retained in the Herbarium of the University of Michigan, Ann Arbor.

[2] Determined by Pippen.

[3] Determined by B. L. Turner, here published.

[4] Determined by Kruckeberg *in* Ornduff et al. 1963.

Senecioneae, including the cacalioid ones, are contrasted by Belcher (1956).

All of these species are herbaceous perennials, flowering from July to December. The perennial caudex and/or roots survive the dry season but the aerial portions wither soon after flowering. The first season of growth is strictly vegetative. A basal rosette of leaves forms in *Odontotrichum* and *Psacalium;* in *Digitacalia* and *Pericalia* a nonflowering, leafy stem develops. Flowering may occur during the second and succeeding years.

Leaves in all of the genera are petiolate (except certain specimens of *Pericalia sessilifolia*). The leaves are usually fleshy or coriaceous with prominently convex veins usually more pronounced on the abaxial surface. In several species of *Odontotrichum* (*O. pachyphyllum*, *O. platylepis*, and *O. amplum*) the two surfaces of the leaves are similar with the venation equally pronounced on both surfaces.

The leaf shapes and patterns of lobing are relatively constant, although wide ranges of variation may occur within the limits of some species (e.g., *Odontotrichum sinuatum*) and occasional parallel leaf forms between species (*O. silphiifolium* and *O. goldsmithii*). In general, however, each species may be recognized by a characteristic leaf shape

and pattern of lobing. The venation is mostly pinnate, subpalmate, or radiate (the latter in *Psacalium* only).

In *Odontotrichum* the form of the leaves exhibits a series ranging from entire or toothed (as in *O. amplum*, *O. pachyphyllum*, and *O. silphiifolium*) to lobed (*O. sinuatum*, *O. pringlei*, and *O. multilobum*) and pinnatisect (*O. decompositum*). This series in general parallels a reduction in the size of heads and size of inflorescence bracts.

The inflorescences are monochasial (Rickett, 1955) with at least 5 heads. They may be corymbose, paniculate, or less frequently racemose. The bracts subtending the branches of the inflorescence and the calyculate bracts are relatively constant within a species and either small, linear-subulate or larger and leafy. The leafy inflorescence bracts are usually vaginate or naviculate and clasping the stem or in some species, petiolate.

Heads are always discoid with perfect and fertile flowers. The size of the heads, as determined by the number of phyllaries and flowers, is relatively constant within each species.

The flowers are nearly white or cream colored, often with a greenish or purplish tint but never yellow or orange. The corolla tube is narrowly cylindrical and usually as long as or longer than the lobes of the limb. The limb is divided into 5 equal lobes that are usually free to the base of the limb or, in some species, connate for part of their length into an ampliate, campanulate, or funnelform throat. The throat is usually shorter than the lobes or, less frequently, as long as the lobes (longer than the lobes only in *Pericalia michoacana*).

This condition of the corolla is referred to as the "cacalioid condition" to distinguish it from that found in *Senecio* where the corolla throat is much longer than the lobes, the latter forming only five small, deltoid, ascending teeth above the throat—referred to as the "senecioid condition" (fig. 1).

The achenes vary from ellipsoid, obovoid and dorsally compressed, elliptic or ovate in cross section (*Odontotrichum* and *Psacalium*) to oblong, subcylindrical, and subterete in cross section (*Digitacalia* and *Pericalia*). The surface is usually narrowly striated or often prominently 10- to 12-ribbed. In several species the achenes are pubescent with simple unicellular hairs but none of the species has hygroscopic trichomes like those found on achenes of several species of *Senecio*.

The pappus consists of a single row of many, persistent (deciduous in *Odontotrichum cirsiifolium*), white or cream colored, stiff, barbellate, capillary bristles (as in most of the Senecioneae). They are usually as long as the corolla or occasionally much shorter and stiffer (*O. brachycomum* and *O. palmeri*), or even entirely lacking (*Psacalium calvum* and *P. nanum*).

A study of pollen grains of representative species (mounted in lactic

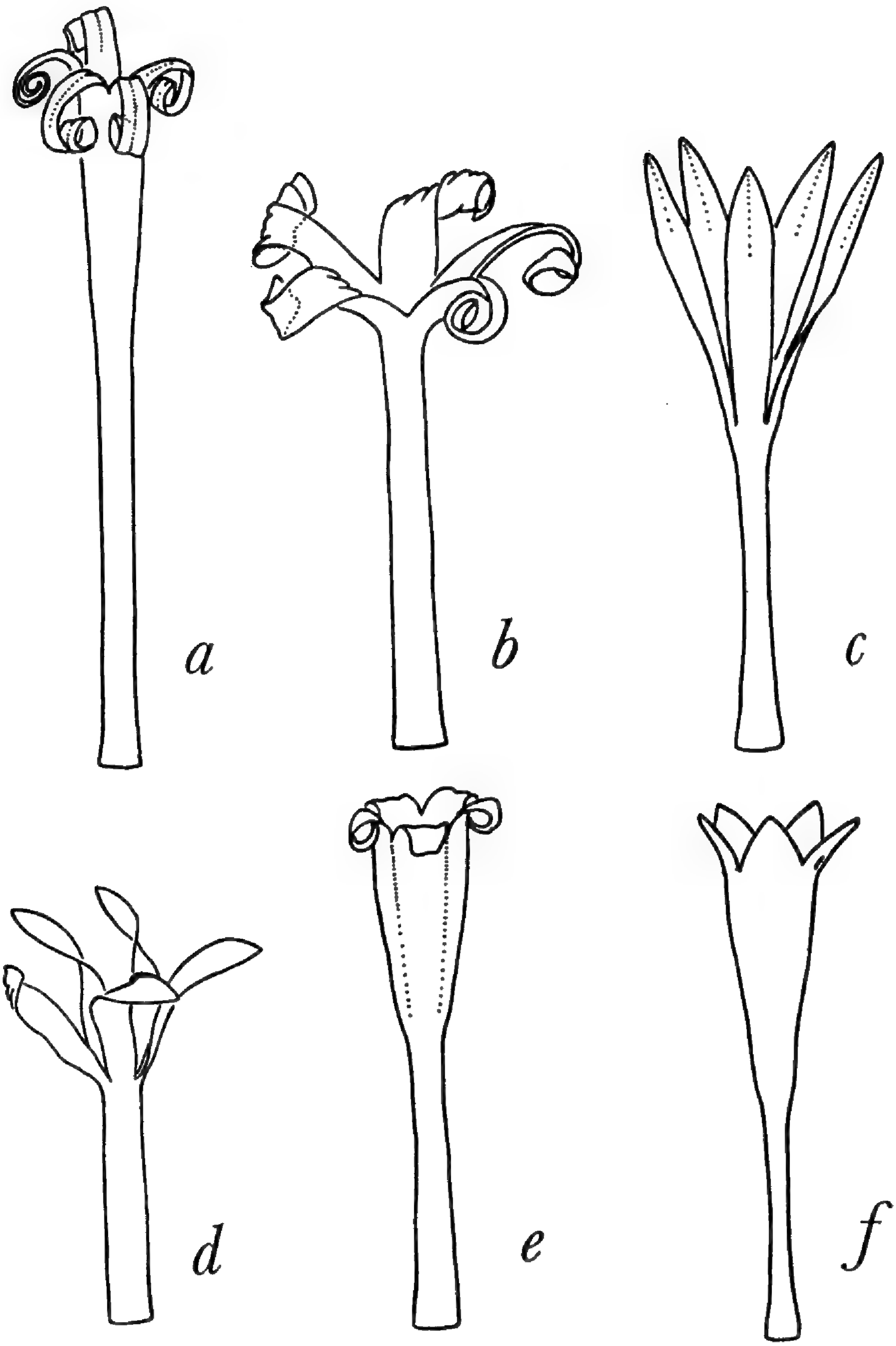

FIGURE 1.—Types of discoid corollas (all ×10): *a. Pericalia sessilifolia* (*Pippen* 64, MICH); *b. Psacalium peltatum* var. typ. (*Pippen* 49, MICH); *c. Odontotrichum sinuatum* (*Pippen* 22, MICH); *d. Digitacalia jatrophoides* (*L. C. Smith* 123, MICH); *e. Senecio angulifolius* (sect. *Palmatinervii*) (*McVaugh* 9949, MICH); *f. Senecio callosus* (sect. *Mulgedifolii*) (*Hurd* 36, MICH).

acid or Hoyer's medium) revealed a similarity in all four genera. The grains are spherical, tricolpate, 42–45 microns in diameter. The surface is ornamented with simple spines 7 to 9 microns long.

Several species exhibit various degrees of pubescence, the presence or absence of which on organs such as leaves, achenes, and phyllaries is relatively constant for each species. The trichomes are mostly nonglandular, conical-attenuate, white or hyaline, multicellular, frequently with purple crosswalls. They vary in length, number of cells, stiffness, and density. Occasionally the distal end of the hair is prolonged into a caudate tip as long as or longer than the body. A minute stipitate gland, ca. 0.5 mm. long, consisting of a stalk of several cells in a single row, topped with a multicellular, globose, purple gland occurs mixed among the longer, nonglandular hairs in several species of *Psacalium*.

Distribution and Ecology

The genera *Digitacalia*, *Odontotrichum*, *Pericalia*, and *Psacalium* are all endemic to Mexico, except that one species, *Odontotrichum decompositum*, extends northward into the mountains of southern Arizona. The species of all four genera are restricted mostly to the oak-pine zone, which is extensively developed in the higher mountain regions of Mexico. Within this zone the species of *Odontotrichum* and *Digitacalia* are usually associated with the grasslands or oak savannahs and *Pericalia* and *Psacalium* with the open oak-pine woods or their borders. But species of the different genera do not usually grow together in the same community.

The annual seasonal pattern in the oak-pine woodland zone is one of alternating wet and dry periods. The rainy season often begins in May and continues as late as October in certain areas, the peak reached during July and August. The dry season lasts from about mid-November until mid-May. The highest temperatures are usually reached during the months just prior to the peak of the rainy season, April through June (Contreras Arias, 1942). The active growing period corresponds to the rainy season with little plant growth during the dry season when the plants die or remain dormant.

Most of these taxa occur at altitudes between 1,000 and 3,000 meters, although a few specimens have been collected at elevations as low as 350 meters. These plants seem to thrive in disturbed secondary associations such as grazed grasslands, burned-over woodlands, or roadsides. Originally they probably grew along the margins of the oak-pine woods or in natural openings within the woods. The majority of the species grow in well-drained rocky, clay soils but a few species do well in poorly drained, similar soils.

The region of greatest concentration of these species corresponds closely to the Trans-Mexican volcanic belt (Clausen, 1959) or Neo-

volcanic Plateau (Raisz, 1959). This zone extends from the region of Orizaba, in Veracruz, through the region of Mexico City to western Michoacán, thence curving northward toward Guadalajara and again northwestward toward Tepic. In all directions away from this zone the number of species diminishes rapidly. Other centers of concentration for *Digitacalia*, *Odontotrichum*, and *Psacalium* are in southern Durango and central Oaxaca, in the latter region are several endemic taxa.

The general distributional patterns within Mexico are illustrated in figures 2 and 3.

Generic Relationships and Evolution

The genera *Digitacalia*, *Odontotrichum*, *Pericalia*, and *Psacalium* are apparently natural genera, possibly having closer relationships to separate elements within the genus *Senecio* than to each other. Still, these segregate cacalioid genera may be distinguished as a group from *Senecio* by a number of relatively constant characters if the characters are applied collectively (table 2). *Odontotrichum* is the largest genus in the complex. It may be distinguished from the other cacalioid genera by the subscapose habit, the erect, nonpeltate basal leaves, and

TABLE 2.—*Comparison of cacalioid genera and* Senecio

Cacalioid Genera	*Senecio*
(a) Heads always discoid, the flowers all regular and perfect.	(a) Heads radiate or discoid, the ray flowers pistillate; the discoid flowers regular and perfect.
(b) Corollas always creamy or nearly white, never yellow.	(b) Corollas mostly yellow or purple, occasionally creamy or nearly white.
(c) Corollas deeply lobed, the lobes extending to the base of the limb or connate into a throat rarely as long as the free lobes.	(c) Corollas mostly shallowly lobed, the lobes usually less than half as long as the throat.
(d) Achenes mostly obovate or ellipsoid, elliptic in cross section, less frequently cylindric and subterete in cross section; glabrous or pubescent, the hairs never hygroscopic.	(d) Achenes mostly cylindric, subterete in cross section; glabrous or pubescent, the hairs in many species hygroscopic.
(e) Involucre mostly campanulate or turbinate, less frequently cylindrical.	(e) Involucre cylindrical, less frequently campanulate or turbinate.
(f) Plants all herbaceous perennials.	(f) Plants annuals, biennials, herbaceous perennials, shrubs or trees.

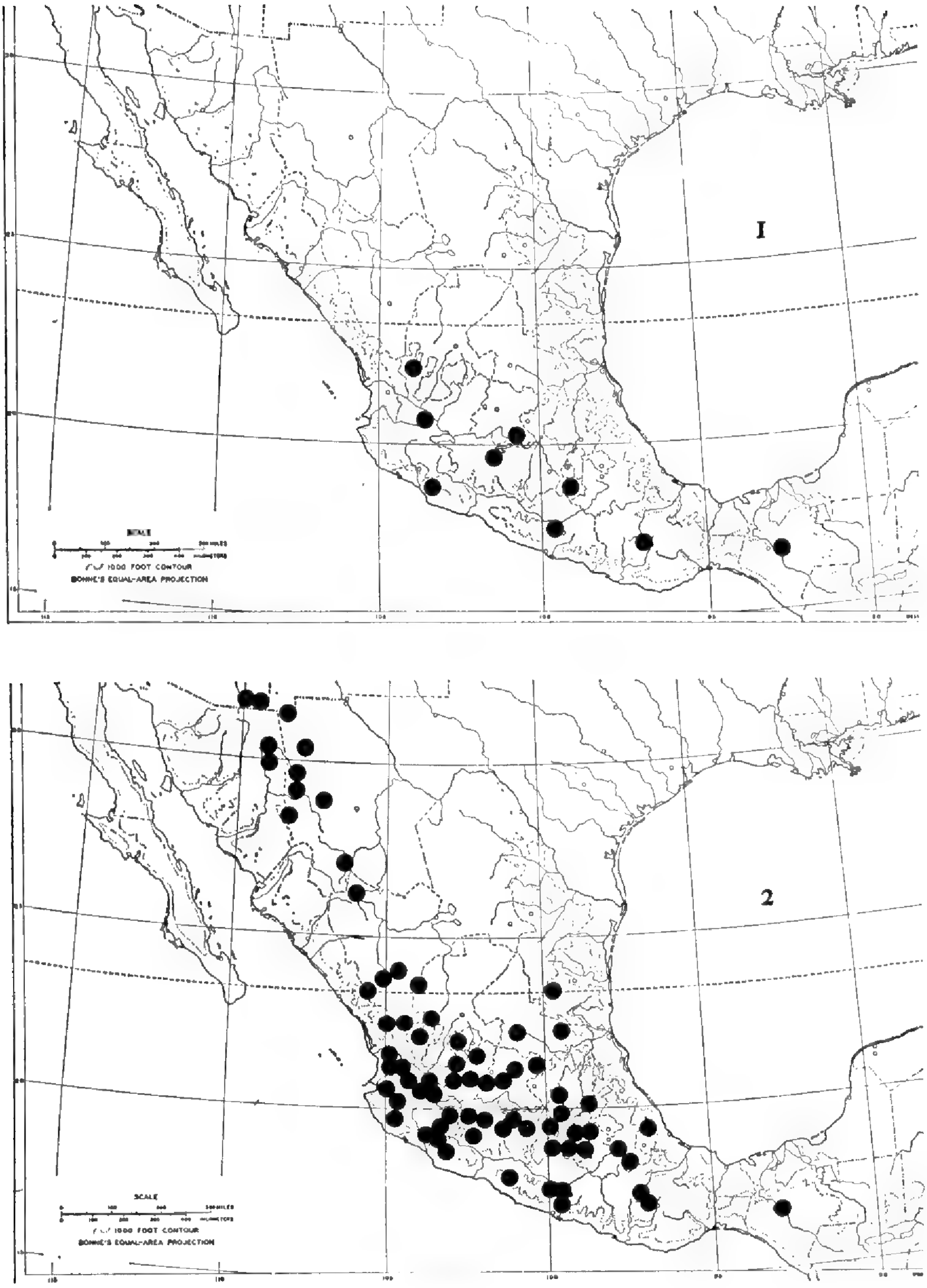

FIGURE 2.—Distribution maps of the Mexican cacalioid genera:
1. *Digitacalia*; 2. *Odontotrichum*.
●=Collection of one or more species.

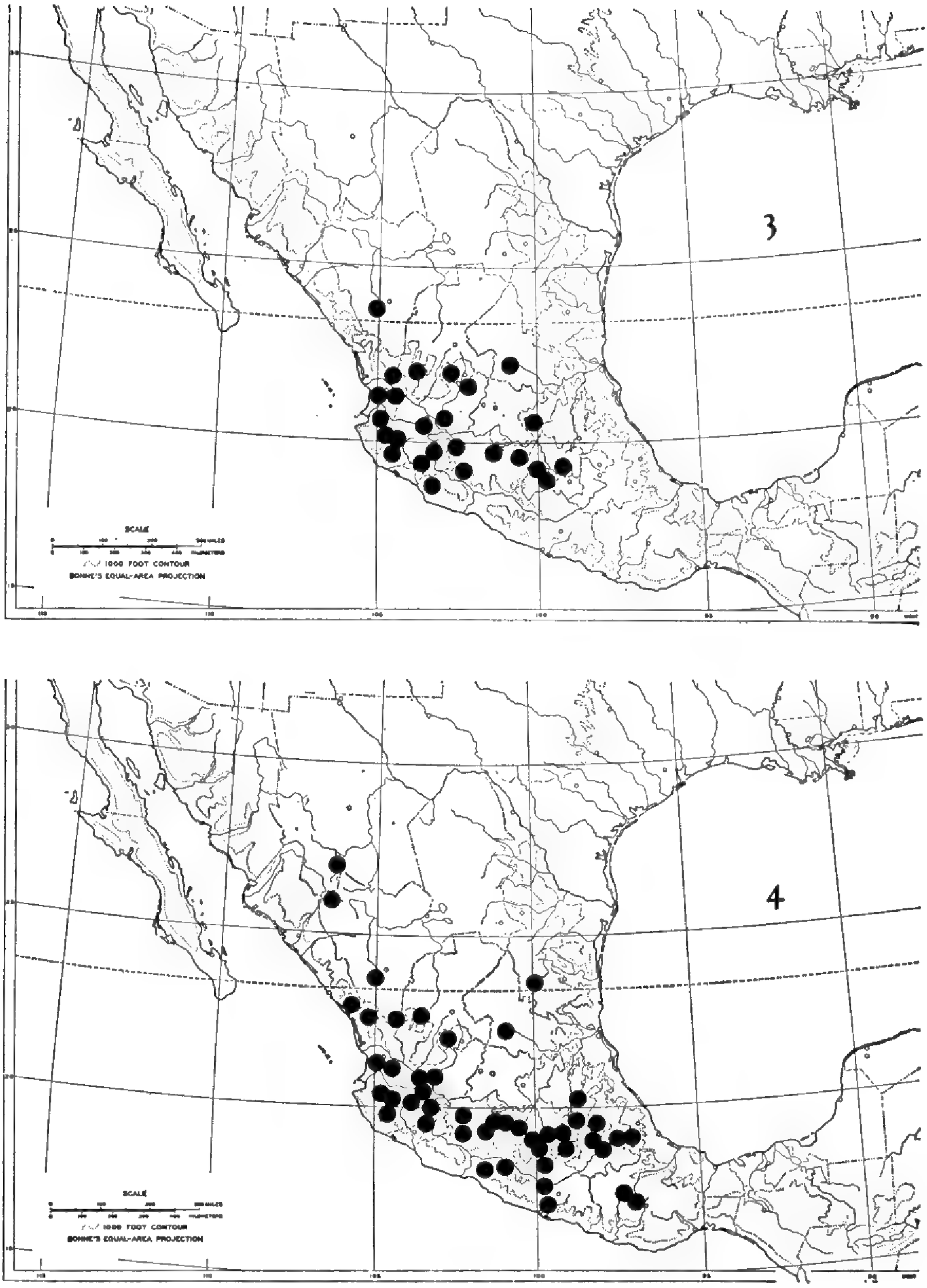

FIGURE 3.—Distribution maps of the Mexican cacalioid genera:
3. *Pericalia*; 4. *Psacalium*.
●=Collection of one or more species.

the corolla lobes free to the base of the limb (fig. 1). Taxa of this description apparently have no counterpart in *Senecio* unless it is in *S.* sect. *Mulgedifolii*. The species in this section have discoid heads usually of purple flowers (although some white-flowered forms do occur) but the corolla throat is much longer than the lobes, the lobes forming only five small, deltoid teeth above the throat (fig. 1). The leaves are mostly membranaceous, narrowly ovate or oblong, regularly callose-dentate, and often runcinate or lyrate-pinnatifid. Several of these species have been described as cacalias (sensu latu), e.g., *S. callosus* Greenm., *S. coulteri* Greenm., *S. runcinatus* Less., *S. purpurascens* Klatt, and *S. deformans* Klatt.

Psacalium is the most distinctive genus of the complex because of the centrally peltate leaves. It is further distinguished by the frequent occurrence of stipitate, glandular trichomes in the inflorescence and the fusion of the corolla lobes into a short throat ca. 1 mm. long (fig. 1). No group of species in *Senecio* is known to be comparable to the species of *Psacalium*, although several species in *S.* sect. *Palmatinervii* appear closely allied. *Senecio subpeltatus* Schultz Bip. and *S. cordobensis* Hemsl. have peltate leaves but the flowers are typically senecioid and the plants are woody shrubs. *Senecio angulifolius* DC. is similar in several respects to *P. peltatum;* the two have leafy inflorescence bracts, heads of approximately the same size, glandular-pubescent stems, and a chromosome number reported as $n=30$. However, *S. angulifolius* is a woody shrub, the leaves are not peltate, the heads are usually radiate (occasionally discoid), and the flowers are always yellow.

Since this group of senecios appears to be somewhat transitional between *Senecio* and *Psacalium*, it is possible that the latter was derived from an ancestral stock that also gave rise to species like those in *S.* sect. *Palmatinervii*.

In *Digitacalia* the plants are leafy stemmed and the upper leaves reduced but not bracteiform. There is neither a basal rosette of leaves nor subterranean tubercles. The corolla is mostly deeply cleft (fig. 1), but the achenes are subcylindric, subterete in cross section, and thus tending toward the senecioid type. *Senecio roldana* DC. and *S. jaliscana* S. Wats. resemble the species of *Digitacalia* in habit, although the leaves are less deeply lobed, but in floral characters they are distinctly senecioid; *S. jaliscana* has discoid heads of orange flowers and *S. roldana* radiate heads of yellow or white flowers. In both species the corollas are senecioid.

Conceivably *Digitacalia* may have been derived from the same ancestral stock that also gave rise to species in *Senecio* like those just discussed.

Finally, *Pericalia* is unique in the cacalioid complex because of its leafy-stemmed habit, the distal bracteiform leaves, the fleshy sub-

terranean tubercles, the numerous (8–15) calyculate bracts, and the well developed, long corolla throat with relatively long, recurved corolla lobes. This genus contains only two species and these have no apparent counterpart in *Senecio*. But *S. hartwegii* Benth. and *S. seemanii* Schultz Bip. (sect. *Palmatinervii*) have certain similarities in vegetative structure to the species of *Pericalia*, although the heads of these senecios are much smaller and distinctly senecioid.

A Central American species, *Senecio cooperi* Greenm. (sect. *Multinervii*), has disk florets similar to the discoid flowers of the cacalioid genera, with the corolla lobes much longer than the throat. The heads, however, are radiate, the flowers yellow, the phyllaries narrowly oblong and barely overlapping, and the leaves lyrate-pinnatifid. This combination of characters definitely associates the species with *Senecio*.

The hypothetical relationship of the cacalioid genera to each other and to the closely allied species of *Senecio* is summarized in figure 4.

It is also apparent that the Mexican cacalioid taxa are not the same as those in the eastern United States (*Cacalia* sect. *Conophora* DC.) or those in eastern Asia (*C.* sect. *Eucacalia* DC.). Further studies of these groups are necessary to determine their proper relationships and taxonomic position.

The 7 or 8 species usually referred to *Cacalia* sect. *Conophora* DC. form a natural group endemic to the eastern United States and southern Canada. These are easily distinguished from the taxa included in this paper as well as from *Senecio* by: The presence of a prolonged chaffy scale forming a beak up to two millimeters long in the center of the receptacle; the consistently small heads with 5 phyllaries and 5 or 6 flowers; the entire or dentate but not lobed, glabrous or glaucous leaves; and the haploid chromosome number of usually 25.

The 8 to 10 species that most earlier workers referred to *C.* sect. *Eucacalia* comprise a natural group mostly endemic to eastern Asia, with the exception of *C. suaveolens* L. which is found only in the eastern United States. These differ from the Mexican members of this complex in: The lack of tufts of hair at the base of the basal leaves; the narrowly paniculate inflorescence; the short corolla tube; and the throat of the corolla equaling or exceeding the corolla lobes in length.

The genus *Cacalia* proper, a small group of central European species typified by *C. alpina* L. (see discussion to follow) differs from the taxa discussed in this paper primarily as follows: The style branches are long-attenuate, the abaxial surface uniformly densely glandular-papillose; the corolla is usually 4-parted; the chromosome number is reported as $n=19$ (Langlet, 1936); and these taxa, under

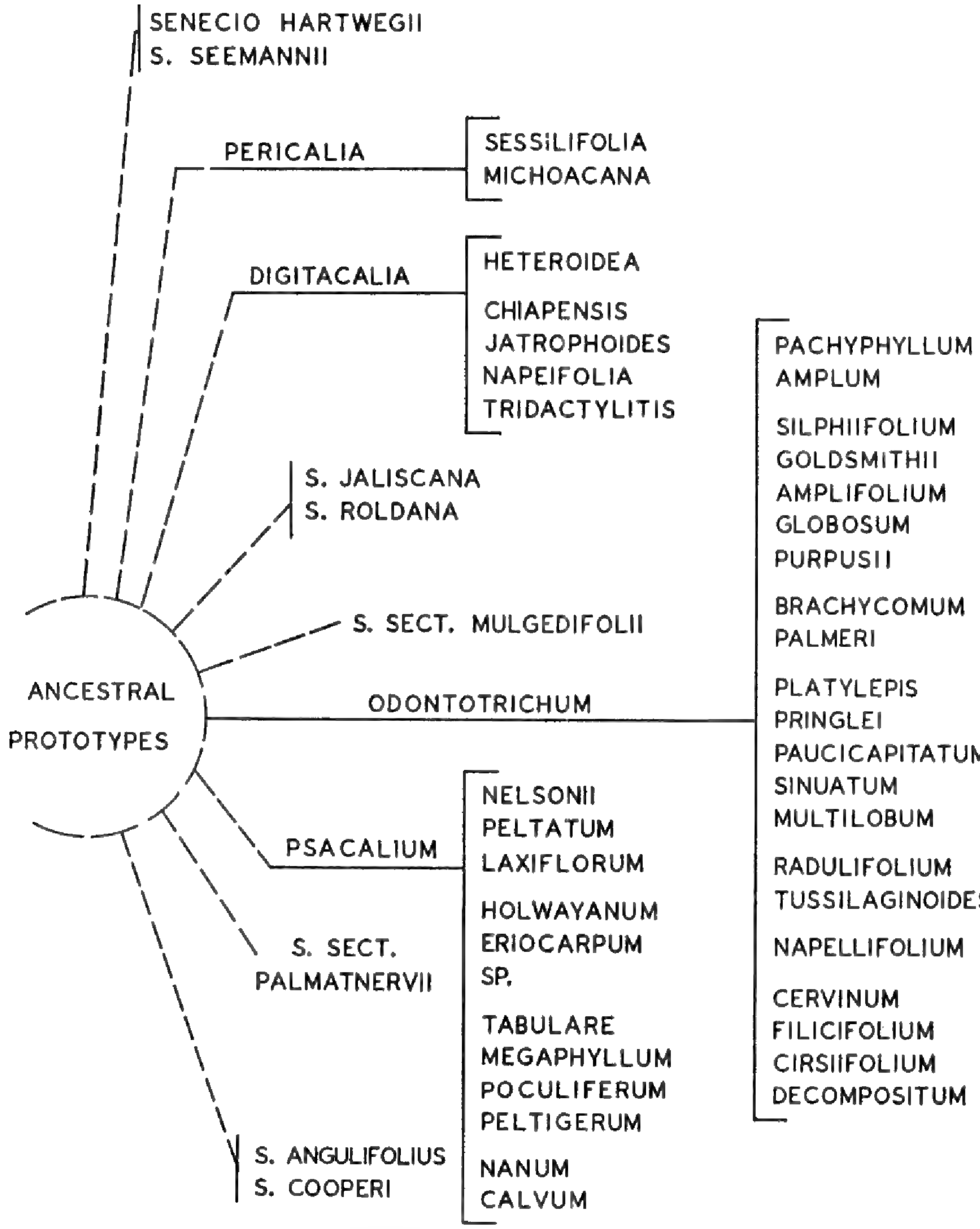

FIGURE 4.—Hypothetical relationships of the species of the cacalioid genera in Mexico to each other and to certain closely allied species of *Senecio*. Vertical gaps and positions represent relative morphological diversity among species and groups of species.

the name *Adenostyles*, have been referred to the tribe Eupatorieae (Hoffmann, 1890).

Nomenclature of *Cacalia*

One of the major points of difficulty concerning the generic nomenclature of the taxa considered in this paper as well as that of *Cacalia* has been the typification of the latter, since no type-species was designated by Linnaeus. The problem of the typification of *Cacalia* has

been reviewed several times (Rydberg, 1924; Hitchcock & Green, 1947; Shinners, 1950; Cuatrecasas, 1960) and therefore does not need to be repeated in detail here. It seems clear that *C. alpina* L. is the most logical lectotype of *Cacalia*. This species, named *C. alpina* by Linnaeus (1753), embodied the Linnaean and pre-Linnaean concept of *Cacalia* in that essentially all of the species of *Cacalia* described by the pre-Linnaean botanists (L'Obel, 1581; Clusius, 1601; Bauhin, 1623; Morison, 1699; Tournefort, 1700) actually represented the same species.

Linnaeus's concept of *Cacalia* was an inclusive one, and a number of the species he considered in this genus were transferred to other genera (Haworth, 1812; Cassini, 1816, 1826, 1827). Nomenclatural difficulty began when Cassini (1816) created a new genus, *Adenostyles*, for a small group of central European plants including *C. alpina* L. as the type-species. *Adenostyles* was actually superfluous when published since the name *Cacalia* should have been used for the genus containing *C. alpina*.

The name *Adenostyles* has been generally accepted (DeCandolle, 1838; Bentham and Hooker, 1873; Hoffmann, 1890; Hegi, 1917; Fiori, 1933) for *C. alpina* and four or five other species endemic to central Europe.

DeCandolle (1838) summarized the work of Cassini and the other post-Linnaean authors. He completely revised the cacalioid complex and in effect retypified *Cacalia*, although he designated no type-species. He divided *Cacalia* into four sections: *Eucacalia* and *Conophora* and two others that he considered doubtfully valid, *Aulacophora* and *Cissampelopsis* (the latter two comprised of several shrubby paleotropical yellow-flowered species now mostly referred to *Senecio*). In the emended genus *Cacalia*, he retained only three Linnaean species, *C. hastata* and *C. suaveolens* in *Eucacalia*, and *C. atriplicifolia* in *Conophora*. DeCandolle recognized Cassini's genus *Adenostyles*, thereby excluding from *Cacalia* the Linnaean type of the genus; he used the name *Psacalium* Cass. for the Mexican species with peltate leaves; and he referred to *Cacalia* various species now properly referred to the genera *Digitacalia*, *Odontotrichum*, *Pericalia*, and *Psacalium*.

In the sense of DeCandolle, therefore, *Cacalia* was to be typified by one of three Linnaean species (but not the logical generic type). It included a variety of species, occurring in Asia, eastern North America, and Mexico, that differed consistently from *Senecio* in a number of respects and was regarded by most authors (Gray, 1883; Hoffmann, 1890; Greenman, 1902; Fernald, 1950; Blake, 1960; Makino, 1958; Cronquist and Gleason, 1963) as comprising a single widespread genus. On the other hand, several authors (Schultz, 1845; Bentham & Hooker, 1873; Hemsley, 1881) did not accept the Candollean *Cacalia*,

preferring to relegate all of the species to *Senecio*. Some authors (e.g., Rydberg, 1924; Cuatrecasas, 1960) took the position accepted in this paper, that of recognizing several valid genera in the Candollean *Cacalia*.

Systematic Treatment

Key to Mexican "Cacalioid" Genera Allied to *Senecio*

1. Basal rosette present, the cauline leaves reduced upward, the uppermost usually bracteiform.
   2. Basal leaves centrally peltate . . . . . **4. Psacalium**
   2. Basal leaves not centrally peltate, the petiole attached to the blade at the edge (subpeltate in *O. radulifolium*) . . . . . **2. Odontotrichum**
1. Basal rosette lacking, the plants with only cauline leaves, the uppermost leaves reduced but not bracteiform.
   3. Plants with underground tubercles attached to the base of the stem; heads subtended by 8–15 linear bracts as long as or longer than the phyllaries. **3. Pericalia**
   3. Plants lacking underground tubercles; heads subtended by 3–5 subulate bracts shorter than the phyllaries . . . . . **1. Digitacalia**

1. Digitacalia

Digitacalia Pippen, gen. nov.

Plantae caulescentes, tuberculis subterraneis nullis, caulibus foliisque glabris vel pubescentibus, foliis omnibus caulinibus, alternis, numerosis, laminis profunde lobatis; inflorescentia corymbosa ampla 30 cm. longa vel longior; capitula numerosa, breves, corollis profunde 5-lobatis, lobis saepe basin versus connatis; achaenia oblonga, subteretia; pappus sordidus.

Typus: *Cacalia jatrophoides* H.B.K.

Perennial, leafy-stemmed herbs to 3 m. tall; roots fibrous, fleshy; stems annual, erect, stout, terete or less frequently angulate, glabrous or pubescent, not tuberculate at base; leaves cauline, not forming a basal rosette, alternate, numerous, uniformly distributed along the stem, not clustered toward the middle, the uppermost not bracteiform; blades shaped variously, deeply pinnately subpalmately lobed; inflorescence corymbose, large, at least 30 cm. long and broad, the branches subtended by small, linear-subulate or large, leafy bracts; heads many, small (except *D. heteroidea*), calyculate, the bracts 3–7, usually shorter than the phyllaries; involucre campanulate or turbinate, the phyllaries 5–8, biseriate appearing uniseriate, imbricate, the overlapped margins subscarious, the exposed surface glabrous or pubescent, the tips fringed with minute, nonglandular trichomes up to 0.3 mm. long; receptacle flat or nearly so, alveolate, not paleaceous; flowers all discoid, perfect, fertile; corollas glabrous, creamy or nearly white, occasionally greenish or purplish-tinted but never yellow, the

tube narrowly cylindrical, ca. 0.5 mm. in diameter, the limb divided into 5 equal, 3-nerved, narrowly triangular or linear, ascending or spreading lobes, the lobes free to the tube or connate into an ampliate throat up to 1.5 mm. long and broad; anthers 1.5–3 mm. long, exserted from the corolla throat, the bases rounded or slightly sagittate, the terminal appendages trullate or ovate, 0.5–0.7 mm. long; style branches 0.7–2 mm. long, slightly flattened, recurved or spreading, stigmatic over most of the abaxial surfaces, the adaxial surfaces glabrous or hispidulous below, the tips truncate, rounded or obtuse, fringed with unicellular, nonglandular "pollen producing" trichomes, unappendaged; achenes narrowly oblong, subterete in cross section, ribbed; pappus a single row of creamy white, stiff, barbellate, capillary bristles.

This genus differs from *Psacalium* and *Odontotrichum* in that the leaves are strictly cauline with no basal rosette formed and the achenes are essentially cylindrical. It differs from *Pericalia* in that the leaves are not concentrated toward the middle of the stem but more uniformly distributed, there are no underground tubercules and the corolla lobes are not recurved.

Key to Species of *Digitacalia*

1. Heads large, 1.5–2 cm. high at maturity; flowers 40 or more; corolla tube at least twice as long as the lobes . . . . . **2. D. heteroidea**
1. Heads small, 1 cm. high or less; flowers 13 or fewer; corolla tube and lobes about equal.
   2. Achenes pubescent; corollas short, 3–3.5 mm. long . . **1. D. chiapensis**
   2. Achenes glabrous; corollas 5–7 mm. long.
      3. Leaves 3-lobed, the lobes forming an angle, with the midrib, of less than 45 degrees . . . . . **5. D. tridactylitis**
      3. Leaves 5- to 7-lobed, the lobes or at least some of the lobes forming an angle with the midrib greater than 45 degrees.
         4. Phyllaries and flowers 5 or 6 per head . . . . . **4. D. napeifolia**
         4. Phyllaries 7; flowers 8–10 per head . . . . . **3. D. jatrophoides**

1. Digitacalia chiapensis (Hemsl.) Pippen, comb. nov.

Senecio chiapensis Hemsl. Biol. Centr. Amer. Bot. 2:238. 1881. Holotype: Chiapas & c., *Ghiesbreght* 537 (K, not seen; isotype GH!).

Cacalia chiapensis (Hemsl.) A. Gray, Proc. Amer. Acad. 19:53. 1883.

Odontotrichum chiapensis (Hemsl.) Rydb. Bull. Torrey Bot. Club 51:418. 1924.

Lower portion of plant not seen; stems terete, glabrous; leaves presumably all cauline, petiolate, oblong-ovate in outline, 10–14 cm. long, 9–14 cm. wide, pinnately veined; blades deeply pinnately 5-lobed ca. two-thirds the distance to the midrib, the lobes ovate or oblong-acute, 4–6 cm. long, 2–3 cm. wide, about half as wide as long, the lowermost pair of lobes rounded proximally or with two smaller deflected lobules, the margins entire, the abaxial surface

puberulent mostly along the veins, the adaxial surface glabrous; petioles short, to 4 cm. long, glabrous, terete; inflorescence broadly corymbose-paniculate, to 30 cm. long and broad, the branches glabrous, subtended by sessile, ovate bracts; calyculate bracts ca. 3, subulate, 1.5–2 mm. long; heads many, 7–8 mm. long; phyllaries (6 –) 8, glabrous, narrowly ovate, 3.5–5 mm. long, 1–1.5 mm. wide; flowers 9; corolla 3–3.5 mm. long, the tube 1.5–2 mm. long, the lobes linear or narrowly elliptic, 1.5 mm. long, spreading or reflexed, the throat none; anthers 1.5 mm. long; style branches 0.7–1 mm. long, the tips truncate or rounded with a terminal fringe of trichomes; mature achenes not seen, the immature achenes brown, sparsely pubescent; pappus bristles 2–3 mm. long, white.

DISTRIBUTION: Known only from Chiapas. Apparently flowering in the fall but the exact time not known.

This plant has been very poorly collected. It is known from only two collections in Chiapas, one is the type.

CHIAPAS: *Nelson* 3467 (GH, US).

2. Digitacalia heteroidea (Klatt) Pippen, comb. nov.

Senecio heteroideus Klatt, Leopoldina 24:125. 1888. Holotype: Mexico; between San Andrés and San Miguel, *Liebmann* 178 (C, not seen; tracing of type in Klatt's herb. GH!).

Cacalia laevigata Schultz Bip. Leopoldina 24:125. 1888, in synonymy.

Cacalia longipetiolata Rob. & Greenm. Amer. Journ. Sci. III. 50:157. 1895. Holotype: Oaxaca; Sierra de San Felipe, 7,000 ft., Oct. 10, 1894, *C. C. Pringle* 5828 (GH!).

Plants to ca. 2 m. (*Pringle* 6176) tall; lower portion of the plant not seen; stems glabrous, glaucous; leaves pubescent on both surfaces mostly along the veins, presumably all cauline, long-petioled, subpalmately veined with 5–7 principal veins, transversely broadly elliptic in outline, the larger leaves 6–13 cm. long from the basal sinus to the apex, 9.5–22 cm. wide; blades cordate-based, deeply subpalmately 5- to 7-lobed, the lobes oblong or triangular, the larger ones 5–6 cm. long, 1–3 cm. broad, the margins toothed or lobulate; petioles glabrous, terete, 8–12 cm. long; inflorescence paniculate corymbose, the major branches subtended by leafy, narrowly elliptic, petiolate bracts, 3–12 cm. long, 0.5–3 cm. broad, glabrous; pedicels 5–13 cm. long; calyculate bracts 5–7, subulate, 5–7 mm. long; heads 12–40, 16–18 (–20) mm. long; phyllaries 7 or 8, ovate, 11–12 (–14) mm. long, 3–4 (–6) mm. wide, glabrous; receptacle ca. 7 mm. across; flowers ca. 40; corolla 9–10.5 mm. long, the tube 5.5–6 mm. long, the throat short, campanulate, 1–1.5 mm. long, ca. 1.5 mm. across at the apex, the lobes 2–3 mm. long, narrowly triangular, 0.5 mm. wide, loosely reflexed; anthers 3 mm. long; style branches ca. 1 mm. long,

minutely hispid on the abaxial surface, the tips obtuse with a sparse, subterminal fringe of trichomes; mature achenes ellipsoid, 3.5–5.5 mm. long, 1.5 mm. wide, 1 mm. thick, glabrous, brown, with 10–12 prominent, paler ribs; pappus 7–8 mm. long, white.

DISTRIBUTION: Known only from central Oaxaca. Presumably flowering in September or October.

This species is placed in *Digitacalia* because its general habit is like that of the other species in this genus, although the inflorescence with few, large heads of 30 or more flowers is more like the species in *Pericalia.* It differs from *Pericalia* in the short corolla throat and the fewer calyculate bracts. *D. heteroidea* appears to be somewhat intermediate between this genus and *Pericalia.*

OAXACA: *Conzatti* 725 (GH); *Pringle* 6176 (GH, NY, US); *C. L. Smith* 287 (MICH, NY, US).

3. Digitacalia jatrophoides (H.B.K.) Pippen, comb. nov.

Cacalia jatrophoides H.B.K. Nov. Gen. et Sp. 4:169. 1820. (Folio ed. 4:132. 1820.) Holotype: Michoacán; nr Lake Cuitzeo, 900 hex., *Humboldt & Bonpland* 4298 (P, not seen; Field Mus. Neg. 37869!).

Senecio jatrophoides (H.B.K.) Schultz Bip. Flora 28:498. 1845.

Cacalia digitata Sessé & Moc. Pl. N. Hisp. ed. 1. 132. 1889. Lectotype without locality (presumably "in Purulandiri montibus") *Sessé & Moc.* 2826 (MA!; Field Mus. Neg. 42288).

Odontotrichum jatrophoides (H.B.K.) Rydb. Bull. Torrey Bot. Club 51:419. 1924.

Plants to 3 m. tall; stems to 1 cm. thick at the base, mostly hollow, often purplish, glabrous, glaucous; leaves sparsely pubescent on both surfaces mostly along the veins and margins, numerous, long-petiolate, subcircular in outline, 6–10 cm. long and broad, pinnate or subpalmately veined with 5–7 principal veins fused into a common trunk above the base of the blade; blades deeply 5- to 7-lobed, the lobes subpinnate or subpalmate, the central one larger, linear or narrowly ovate, 6–8 cm. long, 1–1.5 cm. wide, the margin subentire or distantly toothed (lobes occasionally larger and the leaves similar to those of *D. napeifolia*); petioles terete, glabrous, purplish, to 9 cm. long; inflorescence broadly corymbose, loose spreading, usually more than 30 cm. long and broad, the branches sparsely pubescent or tomentose, the proximal branches in the axils of the 3-lobed upper leaves, the distal branches subtended by petiolate, narrowly ovate bracts to 2 cm. long; calyculate bracts 3–7, subulate, 2–5 mm. long, heads many, 1–1.5 cm. long; phyllaries 7 or 8, narrowly ovate, 4–5.5 mm. long, 1–1.5 mm. wide, glabrous; flowers 8–10; corolla 6–8 mm. long, the tube greenish, 3–5 mm. long, the lobes 3 mm. long, 0.5 mm. wide, linear or narrowly elliptic, the throat none; anthers ca. 2 mm. long; style branches 1 mm. long, recurved, the tips rounded or obtuse with a subterminal fringe of trichomes; mature achenes narrowly oblong appearing subterete in cross

section, 4–5 mm. long, 1.5 mm. wide, glabrous, pale tan, strongly 10- to 12-ribbed; pappus 5–7 mm. long, creamy, becoming tawny in age.

DISTRIBUTION: Southern Zacatecas and Jalisco, eastward through Michoacán and Guanajuato and south to Oaxaca. Rocky places in highland pastures and grasslands. Flowering in July and August.

The specimens collected in Zacatecas and one from Oaxaca have much broader leaf lobes than the others. These leaf forms are similar to those of *D. napeifolia* DC., but these specimens are considered with *D. jatrophoides* because the floral characters are more like the latter.

GUANAJUATO: *Pringle* 4262 (GH, NY, US). JALISCO: *McVaugh* 17160 (MICH). MICHOACÁN: *Arsène*, s.n., Sept. 9, 1909 (US); *Pippen* 46 (MICH). OAXACA: *L. C. Smith* 123 (GH); *C. L. Smith* 388 (MICH, NY, US); *Pringle* 5741 (GH). ZACATECAS: *Rose* 3040 (GH, US).

4. Digitacalia napeifolia (DC.) Pippen, comb. nov.

Cacalia napeaefolia DC. Prod. 6:328. 1838. Holotype: Oaxaca; summit of San Felipe, in 183–, *Andrieux* 280 (G, not seen; Field Mus. Neg. 33809!).
Senecio napeaefolium (DC.) Schultz Bip. Flora 28:498. 1845.
Odontotrichum napeaefolium (DC.) Rydb. Bull. Torrey Bot. Club 51:418. 1924.

Plants to 2.5 m. tall (*Pringle* 4778); lower portion of the plant not seen; stems terete, purplish, sparsely pubescent; leaves presumably all cauline, numerous, petiolate, pinnately veined, oblong-ovate, 15–29 cm. long, 16–23 cm. wide, progressively smaller upward; blades deeply 5- to 7-lobed to within 0.5–1 cm. of the midrib, the lobes oblong-attenuate, narrowly ovate, to 14 cm. long, 4 cm. wide, the margins finely or coarsely toothed, the proximal pair of lobes usually deflected or at right angles to the midrib, the adaxial surface of the blade glabrous or sparsely pubescent mostly along the veins, the abaxial surface pale, sparsely pubescent or tomentose; petioles subterete, glabrous below becoming pubescent toward the blade; inflorescence corymbose, to 45 cm. long and broad, the branches tomentose, the proximal ones subtended by the uppermost leaves, the distal branches subtended by linear-subulate bracts, 1.5 cm. long; calyculate bracts subulate, 1.5–3 mm. long; heads many, 1 cm. long; phyllaries 5 (rarely 6), oblong or narrowly ovate, 3.5–5.5 mm. long, 1.5–2 mm. wide, glabrous or very sparsely puberulent; flowers 5 or 6; corolla 6–7 mm. long, the tube 3–3.5 mm. long, the lobes 3–4 mm. long, linear or narrowly elliptic, 0.5 mm. wide, the throat none; anthers 2–3 mm. long; style branches 1–2 mm. long, minutely hispid on the abaxial surface, the tips obtuse with a subterminal fringe of trichomes; mature achenes narrowly oblong, appearing subterete in cross section, 4–5 mm. long, 1–1.5 mm. wide, glabrous, purplish brown, strongly 10-ribbed; pappus 6–7 mm. long, creamy, becoming tawny in age.

DISTRIBUTION: Known mostly from central Oaxaca with one col-

lection from Michoacán. Openings in oak-pine woodlands. Flowering in September and October.

MICHOACÁN: *Hinton et al.* 12572 (MICH, NY). OAXACA: *McVaugh* 21823 (MICH); *Nelson* 1133 (GH, US); *Pringle* 4778 (GH, MICH, NY, US).

5. **Digitacalia tridactylitis** (Rob. & Greenm.) Pippen, comb. nov. PLATE 1

Cacalia tridactylitis Rob. & Greenm. Amer. Journ. Sci. III. 50:159. 1895. Holotype: Oaxaca; Sierra de San Felipe, 6,000 ft., Nov. 19, 1894, *C. G. Pringle* 5841 (GH!).

Odontotrichum tridactylitis (Rob. & Greenm.) Rydb. Bull. Torrey Bot. Club 51:419. 1924.

Plants to at least 2.5 m. tall; stems to slightly over 1 cm. thick at the base, angulate or terete, sparsely pubescent below becoming denser above; leaves cauline, numerous, pinnately veined, obtrullate or rhombic in outline, the larger ones 14–20 cm. long, from two-thirds as broad to as long as broad, sparsely pubescent adaxially, gray tomentose on the abaxial surface; blades deeply 3-lobed at least half way to the midrib, the lobes ovate, narrowly ovate or narrowly triangular, variable in size from 2- to 6-times longer than broad, the angle of the lateral lobes to the midrib less than 45 degrees, the margin of the lobes usually entire, occasionally toothed, the base of the blade decurrent along the petiole for a short distance; petioles 2–3.5 cm. long, triangular in cross section, pubescent; inflorescence corymbose, ca. 30 cm. long and broad, the branches tomentose, subtended by the uppermost cauline leaves; pedicels 3–7 mm. long; calyculate bracts 3–7, subulate, 1.5–3.5 mm. long; heads many, 9 mm. long; phyllaries 7 or 8, narrowly ovate, 3.5–4 (–5) mm. long, 1–1.5 mm. wide, glabrous; flowers (7–) 8–10; corolla 5–6 mm. long, the tube 2.5–3 mm. long, the throat usually obsolete or very short, 0.5 mm. long and wide, occasionally to 1.5 mm. long, ca. 1 mm. wide (*McVaugh* 21903), the lobes narrowly elliptic, 2–3 mm. long, 0.5 mm. wide; anthers 2–3 mm. long; style branches 1–1.5 mm. long, the tips rounded with subterminal fringe of trichomes; achenes narrowly oblong, appearing subterete or slightly compressed in cross section, 3.5–4 mm. long, ca. 1 mm. wide, glabrous, pale tan, 10- to 12-ribbed; pappus (3.5–) 4–5.5 mm. long, creamy, slightly clavate distally; chromosome number, $n=30$ (Turner, ined.).

DISTRIBUTION: Morelos, Oaxaca, and Guerrero. Growing in openings in the pine-oak zone. Flowering in October and November.

The specimens from Morelos tend to have deeper, more narrowly lobed leaves and less pubescence on the abaxial surface than the other specimens.

GUERRERO: *McVaugh* 21903* (MICH). MORELOS: *Pringle* 6164 (GH, MICH, NY, US); *Pringle* 9877 (GH, MICH, NY, US). OAXACA: *Nelson* 2080 (US); *C. L. Smith* 380 (MICH, NY); *L. C. Smith* 966 (GH).

2. Odontotrichum

Odontotrichum Zucc. Abhandl. Baier. Akad. Wiss. 1:311. 1832.

Perennial, subscapose herbs, 0.5–2 m. tall; roots fleshy, fibrous, caudex tough, to 5 cm. long, 3 cm. thick, the nodes and terminal buds densely covered with tufts of tawny, long, multicellular hairs; stems usually solitary, annual, erect, slender, terete or less frequently angulate, glabrous or pubescent; radical leaves forming a basal rosette of two to several, the petiole attached to the base of the blade, not centrally peltate; blades pinnately or subpalmately veined, variously lobed or occasionally subentire, glabrous or pubescent; cauline leaves similar to the basal but progressively smaller upward, the uppermost bracteiform; inflorescence paniculate or corymbose often pubescent but not glandular, the branches subtended by small, linear-subulate or large, leafy, often vaginate bracts; heads few to many, calyculate, the bracts usually 1–5, usually as long as or shorter than the phyllaries; involucre cylindrical, campanulate or turbinate, the phyllaries 5–17, imbricate, biseriate appearing uniseriate, the overlapped margins subscarious, the exposed surfaces glabrous or pubescent, the tips fringed with minute trichomes up to 0.3 mm. long; receptacle flat or nearly so, alveolate, occasionally sparsely pubescent, not paleaceous; flowers all discoid, perfect, fertile, 5–80 per head; corollas glabrous, creamy or nearly white, occasionally greenish or purplish tinted but never yellow, the tube narrowly cylindrical, ca. 0.5 mm. in diameter, the limb divided into 5 equal, 3-nerved, narrowly elliptic, narrowly triangular or linear, ascending or spreading, not recurved lobes, the lobes usually free to the tube, occasionally connate into a short, ampliate throat up to 1 mm. long; anthers 2–4 mm. long, exserted above the corolla, the bases rounded or slightly sagittate, the terminal appendages trullate or ovate, 0.5–0.7 mm. long; style branches 0.7–2 mm. long, slightly flattened, recurved or spreading, stigmatic on most of the abaxial surface, the adaxial surface glabrous or hispidulous below, the tips unappendaged, rounded or obtuse, fringed with minute, unicellular, nonglandular, "pollen producing" trichomes; achenes oblong, ellipsoid or obovoid, somewhat dorsally compressed, elliptic or broadly elliptic in cross section, glabrous or pubescent, striate or prominently 10- to 12-ribbed; pappus a single row of white or creamy, stiff, barbellate, capillary bristles; chromosome numbers 25, 30.

TYPE-SPECIES: *Odontotrichum cirsiifolium* Zucc.

This is the largest genus treated in this paper, with 21 species. It is distinguished from *Psacalium* by the lack of centrally peltate leaves, the blades being attached at their bases to the petiole. In most of the species the leaves are vertically oriented, standing erect.

Key to Species of *Odontotrichum*

1. Pappus short, 2 mm. long or less, about half as long as the corolla tube.
   2. Petioles flattened, winged, the margin up to 1 cm. wide; basal leaves lobed about one-half the distance to the midrib, lobes usually longer than broad . . . . . **3. O. brachycomum**
   2. Petioles subterete, not winged; basal leaves coarsely toothed or lobulate, but not lobed, lobules broader than long . . . . . **13. O. palmeri**
1. Pappus at least 3 mm. long, as long as or longer than the corolla tube.
   3. Basal leaves toothed or subentire, not lobed (some species with two auriculate basal lobes formed by the deeply cordate basal sinus).
      4. Inflorescence very compact, globose, 2.5–3 cm. long and broad; phyllaries 5 or 6 per head . . . . . **8. O. globosum**
      4. Inflorescence tightly or loosely corymbose, not globose, at least 4 cm. long and broad; phyllaries at least 7.
         5. Heads large with 30 or more flowers; phyllaries 13 or 14.
            6. Bracts subtending the involucre oblong or obovate, distally laciniate, 3 mm. wide; corolla tube 9–10 mm. long, twice as long as the lobes (5–6 mm. long); phyllaries 12–15 mm. long . . . . **1. O. amplum**
            6. Bracts subtending the involucre linear-subulate, tapering to a point distally; corolla tube 5–6 mm. long, slightly longer than the lobes (3.5–4 mm. long); phyllaries 7–9 mm. long . **12. O. pachyphyllum**
         5. Heads small with 15 or fewer flowers; phyllaries 8 or fewer.
            7. Basal leaves deeply cordate-based; petioles of the cauline leaves broadly leafy-margined, the base auriculate, clasping the stem; corolla tube 5–6 mm. long . . . . . **19. O. silphiifolium**
            7. Basal leaves truncate- or obtuse-based, rarely slightly cordate; petioles of the cauline leaves usually terete, the base dilated but not auriculate or clasping the stem (occasionally the petiole narrowly leafy-margined or the leaves sessile); corolla tube 3–4 mm. long.
               8. Plants 0.6 m. tall or less; basal leaves (including the petiole) 11–17 cm. long . . . . . **17. O. purpusii**
               8. Plants at least 1 m. tall; basal leaves (including the petiole) (15–) 20–39 cm. long.
                  9. Phyllaries 5 or 6; flowers 6 or 7; leaves sparsely puberulent. **9b. O. goldsmithii** var. **rowellii**
                  9. Phyllaries 7 or 8; flowers 9–13; leaves glabrous. **9a. O. goldsmithii** var. **goldsmithii**
   3. Basal leaves pinnately or subpalmately divided into several lobes, the lobes as long as broad or longer.
      10. Leaves deeply dissected or pinnatisect into linear segments, the ultimate segments linear or narrowly triangular, at least 5 times longer than broad.
         11. Median and distal cauline leaves broadly auriculate-based, the margin laciniate; proximal inflorescence bracts ovate, navicular, 1.5–3 cm. long, 2–3 cm. broad, the margin distally laciniate; pappus deciduous before maturity of the achenes . . . . **5. O. cirsiifolium**
      11. Median and distal cauline leaves often dilated at the base but not broadly auriculate-based or laciniate-margined; proximal inflorescence bracts linear-subulate, up to 1.5 cm. long, 1 mm. wide or less; pappus persistent.
         12. Achenes glabrous.

13. Leaves 3- to 4-pinnatisect; heads with 6–8 flowers and 5 or 6 phyllaries . . . . . **6. O. decompositum**
13. Leaves deeply dissected or pinnatifid with the primary divisions again 3- to 5-lobed but not cleft to the midrib; heads with 10 flowers and 8 phyllaries . . . . . **10. O. multilobum**

12. Achenes pubescent.
14. Heads with 12–25 flowers; phyllaries sparsely pubescent. **11. O. napellifolium**
14. Heads with 10 or fewer flowers; phyllaries glabrous.
15. Pappus 7 mm. long, about as long as the corolla (lobes plus tube); phyllaries 5 or 6 . . . . . **7. O. filicifolium**
15. Pappus 3.5–4 mm. long, about as long as the tube of the corolla; phyllaries 7. . . . . **4. O. cervinum**

10. Leaves shallowly or deeply lobed but not finely dissected or pinnatisect into linear segments, the ultimate segments triangular or deltoid, usually less than 3 times longer than broad.
16. Heads large, 1.5–2.5 cm. high with 40 or more flowers; corolla tube 7–10 mm. long, twice as long as the lobes.
17. Bracts subtending the involucre leafy, oblong or obovate, distally laciniate, 3–5 mm. wide; leaves and stem sparsely puberulent; basal leaves 18–75 cm. long and broad . . . . **15. O. platylepis**
17. Bracts subtending the involucre linear-subulate, simple, entire-margined, 1 mm. wide or less, not leafy; leaves and stem densely covered by an interwoven mass of gray white, long trichomes; basal leaves 14–16 cm. long, ca. 10 cm. wide. **14. O. paucicapitatum**

16. Heads small, 1–1.2 cm. high or less; flowers 14 or fewer; corolla tube about equaling the lobes (ca. 5 mm. long).
18. Achenes pubescent.
19. Basal leaves subpeltate, the petiole attached to the blade 2-10 (–30) mm. above the base, the blades 10–12 (–18) cm. long. **18. O. radulifolium**
19. Basal leaves attached at base to petiole, not peltate, the blades 20–30 cm. long.
20. Heads with 9–14 flowers and 7 or 8 phyllaries; cauline leaves reduced, bracteiform, narrowly ovate, laciniate-lobed, 8 cm. long or less, 1–3 cm. broad, the base not auriculate. **16. O. pringlei**
20. Heads with 5 or 6 flowers and 5 phyllaries; cauline leaves broadly ovate, leafy, auriculate-based, 11–20 cm. long, 11–20 cm. broad, the margin dentate or lobed . . **21. O. tussilaginoides**

18. Achenes glabrous.
21. Leaves shallowly lobed, the lobes as long as broad or broader (3–7 cm. broad), rounded at the tip, the margin regularly toothed; petiole of the cauline leaves leafy-margined, broadly ovate, auriculate-based; lower inflorescence bracts leafy, 4–9 cm. long, 1–3 cm. wide, ovate-naviculate . . . . **2. O. amplifolium**
21. Leaves deeply lobed, the lobes longer than broad (1–3 cm. broad), oblong or obovate, each of the lobes irregularly 3- to 5-lobed; petiole of the cauline leaves dilated or often clasping the stem but not broadly leafy-margined or auriculate-based; lower inflorescence bracts narrowly ovate or linear-subulate, 1–1.5 cm. long, 3 mm. wide . . . . . **20. O. sinuatum**

1. Odontotrichum amplum Rydb. Bull. Torrey Bot. Club 51:417. 1924. Holotype: Jalisco; road between Huejuquilla and Mesquitic [Mezquitic], Aug. 25, 1897, *J. N. Rose* 3575 (US!).

Plants 0.7–1 m. tall, glabrous; stem usually one, 5–8 mm. thick at the base, terete, glaucous; basal leaves 2 or 3, coriaceous, long-petioled, deltoid or transversely triangular, the apex rounded, 9–10 cm. long, (11–) 18–19 (–22) cm. wide; blades sagittate-based, coarsely dentate or lobulate, the teeth or lobules many, deltoid or 3-angled, 5–8 (–12) mm. long, 8–10 (–15) mm. wide, ciliate, the abaxial and adaxial surfaces very similar; petioles to 28 (–40) cm. long, terete; cauline leaves 5–6, the lowermost one-half to two-thirds as large as the basal ones and similar to them, the petiole proximally dilated, clasping the stem; upper cauline leaves gradually smaller upward, the petioles broadly leafy-margined, the uppermost forming leafy inflorescence bracts; inflorescence corymbose, 9–23 cm. long, 15–20 cm. broad, glaucous; pedicels 2–6 cm. long; calyculate bracts 3–5, leafy, 1–1.5 cm. long, 3–6 mm. wide, distally 5- to 9-toothed; heads 9–15, 18–25 mm. long; phyllaries 13 (–15), ovate or narrowly ovate, 12–15 mm. long, 4–5.5 mm. wide, glabrous; receptacle 10–12 mm. across; flowers 40–50 or more; corolla 14–16 mm. long, the tube 9–10 mm. long, ca. 0.5 mm. wide, the lobes oblong, acute-tipped, 5–6 mm. long, the throat none; anthers 3.5 mm. long; style branches 1.5 mm. long, the tips truncate with a terminal fringe of trichomes; mature achenes ellipsoid, somewhat dorsally compressed, 6–7 mm. long, 2 mm. wide, ca. 1.5 mm. thick, glabrous, tan, 20- to 22-ribbed; pappus creamy, 8–11 mm. long, chromosome number, $n=30$ (Pippen).

DISTRIBUTION: Western Aguascalientes and southwestern Zacatecas. Grazed grassland areas. Flowering in September.

Known only from four collections. This species is very similar to *O. pachyphyllum* but differs in having larger heads with more flowers and leafy calyculate bracts.

AGUASCALIENTES: *McVaugh & Koelz* 57 (MICH); *Pippen* 2, 3, 4 (MICH). ZACATECAS: *McVaugh* 17726 (MICH).

2. Odontotrichum amplifolium (DC.) Rydb. Bull. Torrey Bot. Club 51:416. 1924.
Cacalia amplifolia DC. Prod. 328. 1838. Holotype: Oaxaca; Sierra de San Felipe, on the summit, July 1832, *G. Andrieux* 293; (G, not seen; Field Mus. Neg. 33808!).
Senecio amplifolius (DC.) Schultz Bip. Flora 28:498. 1845.
Senecio rumicifolius Klatt, Leopoldina 24:126. 1888. Holotype: Mexico; Cumbre de Estepa, September 1842. *Liebmann* 237 (C, not seen; tracing of type in Klatt's Herb., GH!).
Cacalia rumicifolia Schultz Bip. Leopoldina 24:126. 1888, in synonymy.
Odontotrichum rumicifolium (Klatt) Rydb. Bull. Torrey Bot. Club 51:416. 1924.

Plants to 1.5 m. tall; stem 0.5–1 cm. thick at the base, terete arachnoid pubescent, the hairs multicellular, 0.5 mm. long, white, interwoven; leaves sparsely pubescent adaxially, densely pubescent abaxially; basal leaves 2–5, occasionally more, long-petioled, pinnately veined, ovate-cordate or oblong-cordate, (13–) 17–27 (–30) cm. long or longer, (12–) 13–19 (–24) cm. wide or wider, usually ca. two-thirds longer than wide; blades shallowly lobed, the lobes 12–16, rounded, usually broader than long, (1.5–) 3–4 (–5) cm. long, (2.5–) 3–5 (–7) cm. wide, each lobe often shallowly 2- to 3-lobed or coarsely toothed; petioles usually longer than the blade, 20–35 cm. long; cauline leaves 3 or more, the lowermost similar to the basal ones but the petiole leafy-margined and more dilated and clasping at the base; upper cauline leaves progressively smaller upward, the uppermost leaves bracteiform, forming leafy, ovate-naviculate inflorescence bracts, (3–) 4–9 cm. long, 1–3 cm. wide, distally toothed; inflorescence corymbose, (6–) 16–30 cm. long, 10–20 cm. broad, the branches tomentose; pedicels 0.5–1.5 cm. long; calyculate bracts 1–3, subulate, 3–6 mm. long; heads 50 to over 100, 6–10 mm. long; phyllaries 7 or 8 ovate or narrowly ovate, 4–5.5 mm. long, 1–2 mm. wide (specimens from Oaxaca with phyllaries 6–7 mm. long, 2–3 mm. wide), glabrous; flowers (8–) 10–13, corolla (5–) 6.5–7.5 mm. long, the tube (2.5–) 3.5–4 (–5.5) mm. long, the lobes linear, (2–) 3–3.5 mm. long, the throat none; anthers 2–3 mm. long; style branches 1–1.5 mm. long, hispid on the abaxial surface, the tips truncate or obtuse with a terminal or subterminal fringe of trichomes; mature achenes ellipsoid or obovoid (often the marginal ones falcate), 5–5.5 mm. long, 2–3 mm. wide, 1.5–2 mm. thick, glabrous, light brown, striate; pappus creamy, becoming fuscous with age, 4–6 mm. long.

DISTRIBUTION: Oaxaca, Guerrero, and México. Grassy openings in the oak-pine-fir woodlands. Flowering from August to October.

This species is closely related to *O. silphiifolium* and *O. goldsmithii*. The specimens from Guerrero and México differ from those in Oaxaca in that the size of the heads (phyllaries and flowers) tend to be smaller, the inflorescence more open and spreading, and the plants less pubescent.

DISTRITO FEDERAL: *Matuda* 26624 (NY). GUERRERO: *Sharp* 441465 (NY); *Nelson* 2243 (GH, US, this specimen has unusually large leaves); *Rzedowski* 15974, 16015 (MICH). MÉXICO: *Matuda* 27730, 29313, 29609 (NY); *Hinton, et al.* 8349 (MICH). OAXACA: *Purpus* 3139 (GH, NY, US); *Conzatti & Gonzalez* 397 (GH); *L. C. Smith* 124 (GH, this specimen has large cauline leaves and small inflorescence bracts); *Nelson* 1061 (US); *C. L. Smith* 391 (MICH, US); *McVaugh* 21824 (MICH).

3. Odontotrichum brachycomum (Blake) Rydb. Bull. Torrey Bot. Club 51:415. 1924.

Cacalia brachycoma S. F. Blake, Contr. Gray Herb. II. 52:58. 1917. Lectotype: Michoacán; wet ravines near Uruapan, 1,525 m., Nov. 13, 1905, *C. G. Pringle* 10126 (GH!).

Plants 1–2 m. tall; stems terete, 7–9 mm. thick at the base, densely villous below, becoming subglabrous upward, the hairs 0.5–1 mm. long; leaves minutely puberulent mostly along the veins and margins with short, white hairs ca. 0.25 mm. long; basal leaves 3 or 4, coriaceous, long-petioled, mostly deltoid or ovate, 13–19 cm. long or longer and broad, pinnately veined; blades sinuately lobed about one-half the distance to the midrib, the lobes 3–6 cm. long, 2–3.5 cm. wide at the base, each distally divided into 3 lobes, the secondary obes deltoid, 3-angulate, the base of the blade truncate, decurrent along the entire length of the petiole; petiole as long as or longer than the blade, 13–19 cm. long, leafy-margined, the margin up to 5 mm. wide on each side; cauline leaves 3 or 4, the lowermost usually smaller than the basal ones but similar (occasionally larger, more deeply dissected, up to 30 cm. long, 20 cm. wide), the petiole broadly leafy-margined, ovate, dentate, clasping the stem; upper cauline leaves progressively smaller upward, the uppermost bracteiform forming ovate, naviculate inflorescence bracts, 5–8 cm. long, 3–5 cm. wide; inflorescence corymbose, 13–28 cm. long and broad; pedicels to 1 cm. long; calyculate bracts 1–3, subulate, 1–2.5 cm. long, 1–5 mm. wide; heads 50–100, 10–12 mm. long; phyllaries 9, narrowly ovate or oblong, 6–7 mm. long, 1.5–2 mm. wide, glabrous; flowers 10–12 (–14); corolla 6–8 (–10) mm. long, the tube 3–4 mm. long, the lobes linear or narrowly elliptic, 3.5–4 (–6) mm. long, the throat none; anthers 2–3 mm. long; style branches 1 mm. long, the tips truncate with a terminal fringe of trichomes; mature achenes oblong or ellipsoid, (3.5–) 4–6 mm. long, 1 mm. wide, glabrous, brown, 10- to 12-ribbed; pappus 1.5–1.6 mm. long, about half as long as the tube of the corolla, creamy, the bristles unequal; chromosome number, $n=30$ (Turner, ined.).

DISTRIBUTION: Known only from the mountains of western central Michoacán. Grasslands, openings and wet ravines in the oak-pine-woodland zone. Flowering in October.

Blake cited both the *Pringle* 10126 collection at the Gray Herbarium and at the U.S. National Herbarium as the type. *Pringle* 10126 (GH) is chosen as the lectotype because it is annotated in what appears to be Blake's writing, and he was associated with the Gray Herbarium at the time this species was named.

As the name suggests this species has a very short pappus. In *Odontotrichum palmeri* the pappus is as short as in *O. brachycomum* but *O. palmeri* differs in having fewer phyllaries and flowers per head and toothed, but not lobed, basal leaves.

MICHOACÁN: *Hinton et al.* 12146 (MICH, this specimen has an unusually large leaf, NY, US); *Hinton et al.* 15288 (GH, NY, US); *Hinton et al.* 15624 (GH, NY, TEX, US); *King & Soderstrom* 4904 (MICH); *McVaugh* 21934, 21959 (MICH).

4. Odontotrichum cervinum Rydb. Bull. Torrey Bot. Club 51:420. 1924. Holotype: Nayarit; between Pedro Paulo and San Blascito, Aug. 4, 1897, *J. N. Rose* 1986 (US!).

Plants ca. 0.5 m. tall; stem slender, 3–4 mm. thick at the base, subglabrous proximally, becoming sparsely pubescent to tomentose to densely tomentose upward, the hairs white, multicellular; leaves glabrous, the abaxial surface paler; basal leaves 3–5, long-petioled, rhombic or ovate or subcircular in outline, the larger ones about 6–9 cm. long and wide, pinnately veined; blades deeply pinnately dissected into linear divisions, 3–4 mm. wide, the major divisions subdivided several times, the secondary divisions also subdivided; petioles 20–25 cm. long, slender, glabrous, purplish; cauline leaves 3 or 4, the lowermost similar to the basal ones; upper cauline leaves reduced, bracteiform, the uppermost forming inflorescence bracts; inflorescence corymbose, to 10 cm. long and broad, the branches tomentose; pedicels subtended by a linear-subulate bract to 1 cm. long; calyculate bracts linear-subulate, 4–6 mm. long; heads ca. 25 or fewer, 9–10 mm. long; phyllaries 7, oblong-ovate, 5–6 mm. long, 1.5–2.5 mm. wide, glabrous; flowers 8–10; corolla 7–8 mm. long, the tube 3.5–4 mm., the lobes 3.5–4 mm. long, linear or narrowly elliptic, the throat essentially none; anthers dark brown or black, 3 mm. long; style branches 0.7–1 mm. long, the tips truncate with a terminal fringe of trichomes; mature achenes not seen, the immature achenes greenish, sparsely pubescent with white hairs; pappus 3.5–4 mm. long, creamy.

DISTRIBUTION: Known only from Nayarit. Grasslands and borders of fields. Flowering in July.

This taxon is known only from one collection besides the type. It is unusual because of the small, almost subternate leaves. It is related to *O. filicifolium*.

NAYARIT: *McVaugh* 15313 (MICH).

5. Odontotrichum cirsiifolium Zucc. Abhandl. Baier. Akad. Wiss. 1:311. 1832. Holotype: A specimen of a garden plant grown from seeds sent by Karwinski from Mexico (M!; Mich. Neg. 1392). Not *Cacalia cirsiifolia* Hook. & Arn.

Cacalia cervariifolia ["cervariaefolia"] DC. Prod. 6:328. 1838. Holotype: Oaxaca; San Bartolo, *Andrieux* specimen in the DC. herb. (G, not seen; Field Mus. Neg. 28888!).

Senecio cervariaefolius (DC.) Schultz Bip. Flora 28:498. 1845.

Sciadoseris vaginata Kunze, Bot. Zeit. 349. 1851. Holotype: specimen grown in the gardens at Herb. Berol. (not seen).

Mesoneuris bipinnatifida A. Gray, Proc. Amer. Acad. 8:661. 1873. Holotype: Mountain region of Chiapas, *Ghiesbreght* 805 (GH!).

Odontotrichum bipinnatifidum (A. Gray) Rydb. Bull. Torrey Bot. Club 51:413. 1924.

Plants to 1.5 m. tall; stem 4–7 mm. thick at the base, arachnoid-pubescent or tomentose (often flocculent), the hairs white, to 2 mm. long or longer; leaves sparsely pubescent on the adaxial surface, densely pubescent on the abaxial surface; basal leaves 2 or 3, petiolate, elliptic or ovate in outline, 18–25 cm. long, 14–22 cm. wide, usually 2–5 (–10) cm. longer than wide; blades 2 or 3 times pinnatifid, the primary segments 17–21, narrow, opposite proximally becoming alternate distally, 8–12 cm. long, ca. 0.5 cm. wide at the base, each divided into 5–9 lobes, the secondary lobes often lobed or toothed, the ultimate segments narrowly triangular, ca. 1–2.5 cm. long, 1–3 (–7) mm. wide, the rachis narrowly leafy-margined, the margin ca. 1–3 mm. wide; petiole and midrib of the blade not clearly distinguished, the petiole 8–15 cm. long, often narrowly leafy-margined almost to the base, occasionally lobed; cauline leaves 2 or 3, the lowermost similar to the basal ones; upper cauline leaves progressively smaller upward, the bases broadly leafy-margined, auriculate and sheathing the stem, the blades pinnatisect or lobed; inflorescence corymbose, 20–30 cm. long, 10–20 cm. wide, the branches subtended by leafy, ovate-naviculate bracts, 1.5–3 cm. long, 1–2 cm. wide, distally laciniate; pedicels 1.5–4 cm. long; calyculate bracts linear, 3–5, up to 1 cm. long; heads (10–) 30–40 (–50), 10–12 mm. long; phyllaries 11–13, narrowly ovate, (5–) 6–7 (–9) mm. long, 2–3 mm. wide, glabrous; receptacle ca. 3 mm. across; flowers 20–30 (–40); corolla ca. 7 mm. long, the tube 3–3.5 mm. long, the lobes narrowly oblong, (3.5–) 4 (–5) mm. long, the throat none; anthers 3 mm. long; style branches 1–1.5 mm. long, hispid on the abaxial surface, the tips truncate or rounded with a subterminal or terminal fringe of trichomes; mature achenes obovoid, 5.5–6 mm. long, 2–3.5 mm. thick, glabrous (in specimens from Oaxaca and Chiapas) or pubescent with short, unicellular hairs (in specimens from México, Guerrero, and Michoacán), light brown; pappus creamy or tawny, 3–3.5 mm. long, the bristles stiff, deciduous; chromosome number, $n=30$ (Pippen).

DISTRIBUTION: Michoacán, México, Guerrero, and east to Chiapas. Habitat variable: roadside ditches, grasslands, and openings in the oak-woodlands. Flowering in August and September.

This species has two forms distinguished by the presence or absence of pubescence on the achenes and apparently by their somewhat distinct geographical ranges. The specimens from Oaxaca and Chiapas have glabrous achenes whereas those specimens from the north and west of Oaxaca have pubescent achenes. Since no other correlative differences are evident I do not feel that these forms are worth nomenclatural status.

CHIAPAS: *Ghiesbreght* 805 (NY, the leaves of this specimen are not as deeply dissected as the other specimens); *Nelson* 3117 (GH, US). GUERRERO: *Hinton et al.* 9435 (MICH, NY). MÉXICO: *Gilly et al.* 81 (MICH); *Hinton et al.* 8211 (MICH, NY); *Matuda* 28821 (NY); *Karwinski* s.n., September 1827 (M, probable parent of type of *Odontotrichum cirsiifolium* Zucc.). MICHOACÁN: *Pringle* 5272 (GH); *Pippen* 52* (MICH). OAXACA: *Pringle* 4984 (GH, NY, US); *Nelson* 1420 (US); *Galeotti* 2491 (US).

6. Odontotrichum decompositum (A. Gray) Rydb. Bull. Torrey Bot. Club 51:414. 1924.

Cacalia decomposita A. Gray, Pl. Wright. 2:99. 1853. Holotype: Sonora; mountains east of Santa Cruz, September 1851, *Charles Wright* 1286 (GH!).

Senecio grayanus Hemsl. Biol. Centr. Amer. Bot. 2:241. 1881. Name illegitimate.

Mesadenia decomposita (A. Gray) Standley, Contr. U.S. Nat. Herb. 19:749. 1915.

Plants up to 1–1.5 m. tall; stem slender, 3–5 mm. thick at the base, terete, densely pubescent below the lowest leaf with long, multicellular hairs in flocculent patches, becoming subglabrous or sparsely pubescent above the lowest leaf; leaves mostly glabrous or sparsely pubescent, the hairs multicellular, 0.4–1 mm. long, mostly along the veins and margins; basal leaves 2–4, long-petioled, pinnately veined, ovate or elliptic in outline, 20–30 cm. long, 12–27 cm. wide, about as wide as long or usually 2–5 cm. longer than wide; blades 3 or 4 times pinnatisect, the primary divisions 10–15 (–17), opposite below, becoming alternate distally, each 2 or 3 times pinnatisect, the ultimate segments narrowly triangular or narrowly oblong and acute-tipped or falcate, 0.5–2 cm. long, 2–5 mm. wide, the laminar portion of the blade reduced to a narrow margin ca. 1 mm. wide on each side of the main veins; petioles subterete or triangular in cross section, 17–25 cm. long, pubescent below becoming subglabrous or sparsely pubescent distally; cauline leaves 3 or 4, the lowermost one-half as large or as large as the basal ones and similar; upper cauline leaves reduced upward, bracteiform, 4–9 cm. long, 1–4 cm. wide, 1–3 times pinnatisect into linear segments, the uppermost cauline leaf bracts 1–6 cm. long, 5 mm. wide; inflorescence paniculate or corymbose, 11–20 cm. long, 12–22 cm. broad, the branches densely pubescent, the major branches subtended by narrowly ovate or linear-subulate bracts ca. 1.5 cm. long; pedicels 1–1.5 mm. long; calyculate bracts 1–3, 2–4 mm. long, linear-subulate; heads ca. 100 or fewer, 10–12 mm. long; phyllaries 5 or 6 (rarely 8), narrowly ovate, obovate or oblong-acute, (4–) 5–6 (–7) mm. long, (1–) 1.5–2 mm. wide, mostly glabrous or sparsely pubescent; receptacle 1.5 mm. across; flowers (5–) 6–7 (–8); corolla 7–8 (–9) mm. long, the tube 3.5–4 (–5) mm. long, the lobes linear-acute, 3.5–4 mm. long, 0.5 mm. wide, the throat none; anthers 2–3 mm. long; style branches 1–1.5 mm. long, the tips truncate or obtuse with a terminal

fringe of trichomes (or rarely a cluster of trichomes covering the entire tip); mature achenes ellipsoid, often falcate, 4–5 mm. long, 1.5–2 mm. wide, 1 mm. thick, glabrous, dark brown, contrasted with paler ribs, the ribs 15–18; pappus white or creamy, (4–) 5.5–6 (–7) mm. long; chromosome number, $n=30$ (Kruckeberg *in* Ornduff et al., 1963).

DISTRIBUTION: Northwestern Durango, northward into Sonora, Chihuahua, and Arizona. Its southern limit appears to be northern Durango as it has not been found farther south. Grasslands, pastures, and borders of oak-pine woodlands. Flowering in August and September.

This species is unusual because of its several times pinnatisect leaves which have the appearance of being compounded. Of the species of *Odontotrichum* growing in Mexico this one is the most northern in range, extending into southern Arizona.

Odontotrichum decompositum, or "Matarique," as it is called by the natives, is the only species of *Odontotrichum* of known economic importance. It is used medicinally in the treatment of diabetes and other ailments (Martínez, 1959).

ARIZONA: *Barkley* 14A624 (TEX); *Darrow et al.* 1235 (NY); *Eggleston* 10765 (US); *Blumer* 1378 (GH, NY, US); *Kruckeberg* 4644 (MICH); *Darrow*, s.n., July 4, 1937 (NY); *Harrison & Kearney* 6194 (US); 6045 (GH); *Kearney & Peebles* 10092 (US); *Goodding*, s.n., Aug. 28, 1912 (NY); *Goodding* 784 (GH, NY); *Jones* 25053 (GH, NY); *Palmer* s.n., July 1890 (GH, US); *Wilcox* s.n., in 1891 (US). CHIHUAHUA: *Gentry* 1959, 2815 (GH, US); *Hewitt* 68 (GH); *Knobloch* 1293 (MICH); Pringle 767 (GH, MICH, NY, US); *Mearns* 2219 (NY, US), 527, 531 (US, appear to be stunted plants, collected near the summit); *Muller* 3420 (GH); *Nelson* 6095 (GH, US); *Townsend & Barber* 158 (GH, NY, US); *Harde LeSueur* 145 (GH, TEX); *Tucker* 2456 (US); *Townsend* s.n., in 1909 (US); *Gentry* 536M (MICH). DURANGO: *Nelson* 4758 (NY, US). SONORA: *Phillips* 651 (GH, MICH); *White* 2741, 3289, 4353 (GH MICH).

7. Odontotrichum filicifolium Rydb. Bull. Torrey Bot. Club 51:414. 1924. Holotype: Nayarit; between Santa Gertrudis and Santa Teresa, Aug. 8, 1897, *J. N. Rose* 2101 (US!).

Plants up to at least 0.5 m. tall; stem glabrous proximally, sparsely pubescent to tomentose distally; leaves glabrous; basal leaves 2–4, long-petioled, pinnately veined, deltoid or ovate-cordate in outline, 4–5 cm. long and broad; blades deeply and finely dissected, the major divisions several, each divided into smaller segments or lobes, the ultimate segments narrow, linear-attenuate, laminar portion of the blade only a narrow margin, ca. 3–5 mm. wide on each side of the major veins; petioles slender, 11–12 cm. long; cauline leaves 3 or 4, the lowermost smaller than the basal ones but similar; upper cauline leaves bracteiform, dilated at the base, distally laciniate; inflorescence corymbose, the branches tomentose, subtended by narrowly ovate

bracts; calyculate bracts 2 or 3, linear-subulate, 2–4 mm. long; heads 15–25, about 10 mm. long; phyllaries 5 or 6, narrowly ovate, 6–7 mm. long, 2 mm. wide, glabrous; flowers 6–8; corolla ca. 7.5 mm. long, the tube 4 mm. long, the lobes 3.5 mm. long, the throat none; anthers ca. 3 mm. long; style branches 0.7–1 mm. long, hispid on the abaxial surface, the tips obtuse with subterminal fringe of trichomes; mature achenes not seen, the immature achenes densely villous; pappus fuscous, 7 mm. long.

DISTRIBUTION: Known only from the type specimen.

This taxon is quite similar to *Odontotrichum cervinum* and was collected in the same region. It differs from *O. cervinum* in having smaller heads and the larger leaves. Field observations and study of future collections may indicate that these two taxa should be considered as one species.

8. Odontotrichum globosum (Rob. & Fern.) Rydb. Bull. Torrey Bot. Club 51:418. 1924.

Cacalia globosa Rob. & Fern. Proc. Amer. Acad. 30:119. 1894. Holotype: Chihuahua; in a moist meadow, Guachuchic, June 25, 1892, *Hartman* 522 (GH!).

Odontotrichum scabrum Rydb. Bull. Torrey Bot. Club 51:416. 1924.

Cacalia pratensis Standl. Publ. Field Mus. Bot. 22:61. 1940. Holotype: Chihuahua; wet meadows near San Juanito, 2,430 m., July 26, 1937, *F. Shreve* 8031 (F!, isotype MICH!).

Odontotrichum pratense (Standl.) J. Cuatr. Brittonia 8:157. 1955.

Plants 0.5–0.7 (–1.2) m. tall; stem slender, 5 mm. thick or less at the base, mostly subglabrous below becoming sparsely pubescent to arachnoid-tomentose above; leaves glabrous or very sparsely puberulent mostly along the veins; basal leaves 2–4, long-petioled, pinnately veined, cordate or cordate-ovate, 4–7 (–8) cm. long and broad; blades shallowly dentate or entire, the teeth rounded or triangular, the margin of the blade ciliate; petioles glabrous, slender, 12–21 (–30) cm. long; cauline leaves 3 or 4, the lowermost similar to and as large as the basal ones; upper cauline leaves progressively smaller upward, the uppermost bracteiform, leafy, ovate, clasping the stem; inflorescence globose, very compact, 2.5–3 cm. long and broad, the branches arachnoid-tomentose; pedicels 5 mm. long or less; calyculate bracts 1–5, narrowly ovate or linear-subulate, 4–5 mm. long, 1 mm. wide or less; heads about 20, 7–10 mm. long; phyllaries 5 or 6, narrowly ovate or ovate, 5–7 mm. long, 1.5–2 mm. wide, glabrous; flowers (4–) 5–6 (–8); corolla 6–7 (–10) mm. long, the tube 3–3.5 (–5) mm. long, the lobes 3–3.5 (–5) mm. long, 0.5 mm. wide; anthers 2–3 (–3.5) mm. long; style branches ca. 1 mm. long, the tips truncate or obtuse with a subterminal fringe of trichomes; mature achenes pale brown, glabrous; pappus creamy, 3–3.5 (–5) mm. long.

DISTRIBUTION: Chihuahua and Durango. Wet marshy areas in pastured grasslands. Flowering in July and August.

This species is unique because of its habitat—most of the other species in this genus grow in dryer situations—and the very tightly globose inflorescence.

Comparison of the type of *Cacalia pratensis* Standl. with the type of *Odontotrichum globosum* indicates that they are definitely conspecific because they are similar in all respects.

Evidence of natural hybridization between *O. globosum* and *O. sinuatum* was observed by Dr. McVaugh in southern Durango in 1962 and a sampling of these populations was made (voucher specimens, *McVaugh* 21732–21739, MICH). The hybrid population showed various degrees of ecological and morphological intergradation between the two very dissimilar parents.

Odontotrichum scabrum, described by Rydberg from a specimen collected in 1897 (*Rose* 3471, US), is one of these intermediate hybrid forms, resembling *O. globosum* in leaf shape but with a more open inflorescence like *O. sinuatum*. It is not distinct enough to deserve nomenclatural status.

CHIHUAHUA: *Knobloch* 1273 (MICH); *Shreve* 8031 (US); *Gentry* 2785 (MICH, GH, isoparatype of *C. pratensis* Standl.). DURANGO: *Graham* 99 (MICH); *McVaugh* 21732, 21734–21739 (MICH, intermediate forms between *O. globosum* and *O. sinuatum*); *Pennell* 18532 (NY); *Nelson* 4769 (NY); *Rose* 3471 (US, holotype of *O. scabrum* Rydb.).

9. Odontotrichum goldsmithii (B. L. Rob.) Rydb. Bull. Torrey Bot. Club 51:416. 1924.

Cacalia goldsmithii B. L. Rob. Proc. Amer. Acad. 43:45. 1907.

Slender plants to 1 m. tall; stems up to 5 mm. thick at the base, mostly glabrous or sparsely pubescent above; leaves mostly glabrous or sparsely puberulent along the veins and margins; basal leaves 2 or 3, erect, long-petioled, pinnately veined, variable in shape from ovate to broadly ovate, 7–14 (–19) cm. long, 6–12 (–16) cm. wide, as long as wide to twice as long as wide; blades mostly truncate or obtusely based, occasionally slightly cordate, the margins sinuately double-dentate or lobulate, the teeth deltoid-rounded, in two alternating series of large and small respectively; petioles 8–14 (–20) cm. long, slender; cauline leaves ca. 3, the lowermost usually elliptic, as large as or one-half as large as the basal ones and similar; upper cauline leaves greatly reduced, the uppermost bracteiform, leafy, up to 6 cm. long, 0.5–1 cm. wide, the base of the petiole dilated; inflorescence loosely corymbose, 18–23 cm. long, 9–11 cm. broad, the branches densely pubescent, subtended by subulate or narrowly ovate bracts 1–3 cm. long, 1–5 mm. wide, smaller distally; pedicels 5–15 mm. long; calyculate bracts 3 or more, subulate, 1.5–4 mm.

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long; heads 50–75, 10–11 mm. long; phyllaries (5–) 7 or 8, usually ovate-oblong or narrowly ovate, 5–6 (–7) mm. long, (1–) 2–3 mm. wide, glabrous; receptacle up to 1.5 mm. across; flowers 7–13; corolla mostly 6–8 mm. long, the tube 3–4 mm., the lobes 3–4 (–7, *Hinton* 9202) mm. long, narrowly elliptic, strongly 3- (–5-) nerved; anthers 2–3 mm. long; style branches 1 mm. long, usually hispid on the abaxial surface, the tips truncate with a terminal fringe of trichomes; mature achenes ellipsoid, 4–5 mm. long, 2 mm. wide, ca. 1 mm. or less thick, brown, glabrous, 10- to 12-ribbed; pappus creamy white, becoming fuscous in age, 3.5–5 (–7) mm. long.

DISTRIBUTION: Eastern Jalisco to Michoacán and western Guerrero and México. Grasslands and pastures. Flowering in July (and August?).

This species is very closely related to *O. silphiifolium*, and further field and garden study may indicate that they should be considered as the same species. In the present treatment, however, they are recognized as two species with *O. goldsmithii* differing from *O. silphiifolium* in its slender, mostly glabrous habit, open, loose inflorescence with shorter heads, truncate or obtuse leaf bases, and smaller cauline leaves that are not auriculate-based.

Key to Varieties of *O. goldsmithii*

a. Heads with 5 or 6 phyllaries, 6 or 7 flowers; leaves sparsely puberulent.
9b. O. goldsmithii var. rowellii

a. Heads with 7 or 8 phyllaries, 9–13 flowers; leaves glabrous.
9a. O. goldsmithii var. goldsmithii

9a. Odontotrichum goldsmithii var. goldsmithii

Cacalia goldsmithii B. L. Rob. as to Holotype: Jalisco; Hacienda San Marcos, 350 m., July 12, 1905, *P. Goldsmith* 8 (GH!).

Phyllaries mostly 8; flowers 9–13 per head; basal leaves ovate or elliptic, glabrous, the blades truncate or obtuse-based, rarely cordate.

DISTRIBUTION: Jalisco, Michoacán, Guerrero (Mina Distr.), and México.

GUERRERO: *Hinton et al.* 9202 (MICH, NY, this specimen has larger heads than the other specimens). JALISCO: *McVaugh* 15460, 16132 (MICH). MÉXICO: *Hinton* 1266 (MICH); *Hinton et al.* 8066, 7984 (MICH, NY). MICHOACÁN: *Hinton et al.* 5078 (GH, NY, US).

9b. Odontotrichum goldsmithii var. rowellii Pippen var. nov. PLATE 2

A varietas goldsmithii floribus phyllariisque paucis, foliis radicalibus, puberulibus differt.

Heads with 5 or 6 phyllaries, 6 or 7 flowers; basal leaves ovate or narrowly ovate, the blades obtuse or cordate-based, sparsely puberulent.

HOLOTYPE: Guerrero; 1 mi. N. of Agua del Obispo, 3,300 ft., July 1, 1952, *C. M. Rowell, Jr.* 2991 (MICH!).

DISTRIBUTION: Known only from central Guerrero.

This variety is distinguished from the other in the smaller heads with fewer phyllaries and flowers and the somewhat puberulent leaves.

GUERRERO: *Wilkinson & Rowell* 3381 (MICH); *Rhymes & Rowell* 3886 (MICH); *Hicks & Rowell* 3604 (MICH); *Rzedowski* 16073 (MICH); *Sharp* 441431 (NY).

10. Odontotrichum multilobum Pippen, sp. nov. PLATE 3

Plantae tenues ca. 1 m. altae, caule foliisque glabris vel sparse pubescentibus, foliis radicalibus erectis, latis ellipticis 18–30 cm. longis 10–17 cm. latis, profunde pinnatifidis, segmentis principalibus 12–15 linearibus; petiola tenus glabra 10–30 cm. longa; folia culaine bractei, forma 1–2; inflorescentia corymbosa, 16–30 cm. long, 11–16 cm. lata-bracteis 10–20 mm. longis, linearis vel anguste triangularis; capitula 50–100, ca. 12 mm. longa; phyllaria 8, 5–6 (–7) mm. longa, 1.5–2 mm. lata, anguste ovata, glabra; flores 10, corollis 7 mm. longis, tubo lobisque 3.5 mm. longis, achaenis ellipsoidea vel obovata, (3–) 3.5–4 mm. longa, 1.5–2 mm. lata, glabra, pallide fulva; pappus sordidus (5–) 6 (–7) mm. longus.

Plants ca. 1 m. tall; stem and leaves glabrous or sparsely pubescent, becoming sparsely or densely pubescent in the inflorescence; flowering stem 4–6 mm. thick at the base; basal leaves 3 or 4, long-petioled, erect, pinnately veined, broadly elliptic in outline, 18–30 cm. long or longer, 10–17 cm. broad; blade deeply pinnatifid, the laminar portion narrow, ca. 3–6 mm. wide on each side of the vein, the primary lobes 12–15, linear, 7–11 cm. long, each divided into 3–5 major lobes, the secondary lobes either 1- to 2-lobed or coarsely toothed, the ultimate segments linear-acute; angle of the lobes with the midrib less than 90 degrees; petioles ca. 10–30 cm. long, mostly glabrous, triangular in cross section; cauline leaves 1 or 2, similar to the basal leaves but much smaller; inflorescence loosely corymbose, 16–30 cm. long, 11–16 cm. broad, the branches subtended by linear or narrowly triangular bracts 10–20 mm. long, 1–4 wide; calyculate bracts 3–5, subulate, 3–5 mm. long; heads 50–100, ca. 12 mm. long; phyllaries 8, narrowly ovate, 5–6 (–7) mm. long, 1.5–2 mm. wide, glabrous; receptacle 2 mm. across; flowers 10; corolla 7 mm. long, the lobes as long as the tube, 3.5 mm. long, linear, the throat none; anthers 3 mm. long; style branches 1 mm. long, the tips truncate or rounded with a subterminal fringe of trichomes; mature achenes (3–) 3.5–4 mm. long, ellipsoid or obovoid, 1.5–2 mm. wide, 1 mm. thick, glabrous, light brown, ca. 20-striate; pappus (5–) 6 (–7) mm. long, creamy or tawny; chromosome number, $n=30$ (Pippen).

HOLOTYPE: Jalisco; ca. 15 mi. SSE. of Autlán by way of Chante, oak-dominated slopes E. of Mamantlán, ca. 4,500 ft., Aug. 1, 1949, *R. L. & C. R. Wilbur* 2094 (MICH!).

The type specimen is somewhat smaller in stature than the other specimens of the same taxon, but it is representative.

This species is related to *O. pringlei* by the shape of the leaf, but differs in that the achenes are glabrous; and to *O. sinuatum*, differing in the more cylindrical heads, rather than turbinate, and in the lower pair of lobes on the leaves not deflected.

This species is sympatric with *O. pringlei* and *O. palmeri*, possibly intergrading with the latter. Two specimens from western Jalisco (*Pippen* 29, sheets 1 and 2, MICH) are intermediate between *O. multilobum* and *O. palmeri*, suggesting that hybridization may be occurring. At this locality both *O. multilobum* and *O. palmeri* as well as the intermediate forms were growing together, the latter plants mistaken for a third species at the time of collection. Future field studies and examination of additional material are necessary to determine if integration has occurred.

JALISCO: *Pippen* 25, 30*, 29 (possible hybrid between *O. multilobum* and *O. palmeri*), 40 (MICH).

11. Odontotrichum napellifolium (S. Schauer) Rydb. Bull. Torrey Bot. Club. 51:419. 1924.

Cacalia napellifolia S. Schauer, Linnaea 19:732. 1847. Holotype: Mexico; about 1840, *Aschenborn* 312 (B, not seen; tracing of type in Klatt's Herb., GH!).

Plants 0.5–0.6 m. tall; stem slender, 2–4 mm. thick at the base, densely pubescent below, becoming sparsely pubescent upward; leaves mostly glabrous, the margin ciliate; basal leaves 4–7, long-petioled, subpalmately veined with 5–7 principal veins, subcircular in outline, the base cordate, 2.5–5 cm. long from the basal sinus to the tip, 3–8 cm. wide; blades deeply lobed, the primary lobes 3–5 (–7), each deeply divided into 2 or 3 (–4) lobes, the secondary lobes again divided into 3–5 lobules, the ultimate segments narrowly triangular or deltoid, 3–10 mm. long, the proximal pair of lobes deflected, parallel to the petiole, the base of the blade decurrent on the petiole for a short distance; petioles 7–15 cm. long, slender; cauline leaves 1 or 2, the lowermost similar to the basal ones; upper cauline leaves bracteiform, reduced, 2–3 cm. long, 0.5–1 cm. wide, 5- to 7-lobed; inflorescence corymbose, the branches tomentose, the pedicels 0.5–3 cm. long; calyculate bracts about 3, subulate, ca. 4 mm. long; heads 5–8, 10–14 mm. long; phyllaries 10, narrowly ovate, 5–6 mm. long, 1.5–2 mm. wide, sparsely pubescent, the tips purplish; flowers 12–25; corolla 6–7 mm. long, the tube 3–3.5 mm. long; anthers 2.4–3 mm. long; style branches 0.7–1 mm. long, hispid on the abaxial

surface, the tips truncate or obtuse with a subterminal fringe of trichomes; mature achenes ellipsoid, 5 mm. long, 1.5 mm. wide, 1 mm. thick, pale tan or creamy, 10- to 12-ribbed, the ribs pubescent with ascending hairs; pappus creamy, 3–5 mm. long.

DISTRIBUTION: Guerrero and Hidalgo. Grasslands and openings in oak-pine woodlands. Flowering in June and July.

This taxon is distinct because of the small, deeply lobed basal leaves. It is closely related to *O. filicifolium* and *O. cervinum* but differs from both in the larger number of flowers per head.

GUERRERO: *Kubicek & Rowell* 3779 (MICH); *Rhymes & Rowell* 3896 (MICH). HIDALGO: *Pringle* 10024 (MICH, NY, TEX, US); *Salazar* s.n., Aug. 1, 1913 (US).

12. Odontotrichum pachyphyllum (Schultz Bip.) Rydb. Bull. Torrey Bot. Club 51:417. 1924.

Cacalia pachyphylla Schultz Bip. ex Seem. Bot. Voy. Herald. 310. 1856. Holotype: Northwestern Mexico; *Seemann* 1999 (K, not seen; MICH Neg. 622!).

Senecio sclerophyllus Hemsl. Biol. Centr. Amer. Bot. 2:247. 1881. Based on *Cacalia pachyphylla* Schultz Bip. not *S. pachyphyllos* Remy.

Plants 0.5–0.7 m. tall; stem 3–4 mm. thick at the base, pubescent, the hairs white, multicellular, often flocculent; leaves mostly glabrous or sparsely pubescent along the veins; basal leaves 2 or 3, coriaceous, long-petioled, reniform or rounded-deltoid, rarely subcircular in outline (6–) 8–10 (–11) cm. long from the basal sinus to the apex, (10–) 13–18 (–20) cm. wide, the tip broadly rounded, the base truncate or usually shallowly cordate; blades variable, shallowly repandly dentate or subentire, the teeth rounded or obtuse, the adaxial and abaxial surfaces very similar; petioles (4–) 8–18 (–35) cm. long; cauline leaves 2 or more, the lowermost smaller than the basal ones but similar; upper cauline leaves becoming bracteiform upward with the petiole broadly leafy-margined, clasping the stem; inflorescence corymbose, 7–20 cm. long, 7–15 cm. broad, the branches tomentose or villous (glabrous in the type and isotype); pedicels 2–6 cm. long; calyculate bracts 3–5, subulate, 9–13 mm. long, 1 mm. wide, sparsely pubescent; heads 9–15, 1–1.5 cm. long; phyllaries 13 or 14, narrowly ovate, 7–9 mm. long, 1–3 mm. wide, glabrous; flowers 30–35; corolla (7.5–) 8–10 mm. long, the tube (4–) 5–6 mm. long, the throat short, ampliate, up to 0.5 mm. long, 1 mm. wide at the apex, occasionally lacking, the lobes 3.5–4 mm. long; anthers 2–3 mm. long; style branches 1.5 mm. long, the tips truncate or obtuse with a terminal or subterminal fringe of trichomes; mature achenes ellipsoid or oblong, 4–5 mm. long, 2 mm. wide, 1.5 mm. thick, glabrous, brownish, 15- to 16-ribbed; pappus white or tawny, 6–8 mm. long.

DISTRIBUTION: Known only from southern Durango. Openings in pine-oak woodlands. Flowering in August and September.

The type is mostly glabrous with linear inflorescence bracts and large basal leaves with acute basal sinuses. These characteristics are somewhat different from the other specimens studied but the specimens are all similar enough in size of heads, number and size of flowers, texture and general shape of the leaves to be considered part of the same taxon.

This species is closely related to *O. amplum*, differing from it in having smaller heads with narrower inflorescence bracts and basal leaves rounded at the base.

DURANGO: *Gentry* 6969 (MICH, US); *McVaugh* 21659 (MICH); *Pennell* 18332 (NY); *Waterfall* 12668 (MICH); *McVaugh* 21731 (shows possible intergradation with *O. globosum*), 21729 (MICH); *Ownbey & Ownbey* 1874 (MICH, US); *Maysilles* 7784 (MICH). LOCALITY UNKNOWN: *Seemann* s.n. (probably isotype of *Seemann* 1999, GH).

13. Odontotrichum palmeri (Greene) Rydb. Bull. Torrey Bot. Club 51:417. 1924.

Cacalia palmeri E. L. Greene, Pittonia 1:219. 1888. Holotype: Jalisco; Río Blanco, in 1886, *E. Palmer* 168 (ND!, isotypes GH!, US!, NY!).

Plants 0.7–1 (–1.5) m. tall; stems 3–5 (–7) mm. thick at the base, sparsely or densely pubescent, rarely subglabrous, hairs 1.5–3 mm. long, stiff, white; leaves sparsely or densely pubescent, the pubescence denser on the abaxial surface; basal leaves 2–3 (–5), pinnately veined, coriaceous, broadly ovate or occasionally subcircular in outline, 9- 17 (–23) cm. long and broad (broadest below the middle); blades coarsely dentate or shallowly lobulate, the lobules up to 1 cm. long, 2 cm. wide, each 3-angulate, mucronate; petioles (5–) 6–15 (–30) cm. long; cauline leaves several, the lowermost as large as or one-half as large as the basal ones and similar, the petiole dilated and clasping the stem at the base, often leafy-margined; upper cauline leaves reduced and bracteiform, the petiolar portion broadly leafy-margined and clasping the stem, the blade portion ovate, dentate; inflorescence corymbose, 9–12 (–18) cm. long, 10–15 cm. broad, the branches sparsely pubescent, the distal branches subtended by narrowly ovate or subulate bracts up to 1.5 mm. long, the proximal branches in the axils of the uppermost leaves; calyculate bracts usually 3, subulate, 5 mm. long or less; heads up to 100, ca. 1 cm. long; phyllaries 5 or 6 (–7), narrowly ovate, 5–7 (–8) mm. long, 1.5 (–3) mm. wide, glabrous or sparsely pubescent, tightly imbricated forming a narrow cylindrical involucre, the tips attenuate; receptacle often sparsely pubescent with long, mult cellular hairs; flowers 5 or 6 (–8); corolla 6.5–9 mm. long, the tube (3–) 3.5–4 mm. long, the lobes 3.5–5 (–5.5) mm. long, the throat none; anthers 2–3 mm. long; style branches 1–1.5 mm. long, the tips truncate or rounded with a terminal fringe of trichomes; mature achenes 3.5–4 mm. long, 1.5–2 mm. wide, ellipsoid, glabrous, prominently 10- to 12-ribbed, the ribs dark red purple, sharply contrasted

by pale golden-tan bands separating them; pappus creamy or white, (1–) 1.5 (–2) mm. long, about one-half as long as the corolla tube; chromosome number, n=about 25 (Pippen).

DISTRIBUTION: Southern Durango, Nayarit, Jalisco, and Michoacán. Common in grasslands, pastures, and borders of oak-pine woodlands. Flowering in August and September.

This species is similar to *O. brachycomum* in having an extremely short pappus but differs in having smaller heads with fewer flowers and phyllaries, and the leaves not lobed.

Rydberg described *Odontotrichum nephrophyllum* from a specimen collected in southern Durango (*Rose* 2248, US). It differs from *O. palmeri* in that the pappus is as long as the corolla tube and the petioles of the basal leaves are densely pubescent. Examination of future collections may indicate that this is distinct from *O. palmeri*, but at the present I do not feel that it is significantly different.

DURANGO: *Rose* 2248 (US). JALISCO: *Diguet* s.n., July 1912 (MICH); *Graham* 124 (MICH); *McVaugh* 20481, 12929 (MICH); *McVaugh & Koelz* 441 (MICH); *King* 3659 (MICH, NY, TEX, US); *Powell & Edmondson* 869 (TEX); *Pringle* 2304 (GH, NY, US); *Pringle* 11500 (GH, MICH, US); *Pippen* 10, 20, 27A, 32, 28 (MICH). MICHOACÁN: *Arsène* 5132 (GH, NY, US); *Feddema* 183 (MICH); *Leavenworth* 539 (NY, MICH); *Pippen* 43 (MICH); *McVaugh* 21960 (MICH). NAYARIT: *Feddema* 308 (MICH); *Pippen* 12* (MICH).

14. Odontotrichum paucicapitatum (Rob. & Greenm.) Rydb. Bull. Torrey Bot. Club 51:414. 1924.

Cacalia paucicapitata Rob. & Greenm. Amer. Journ. Sci. III. 50:158. 1895. Holotype: Oaxaca; Sierra de Clavellinas, 7,000 ft., Oct. 25, 1894, *C. G. Pringle* 6018 (GH!, isotypes GH!, US!).

Plants to 1 m. tall; caudex apparently fleshy, globose, at least 2 cm. long, 2.5 cm. wide; stem ca. 5 mm. thick at the base, densely covered with a flocculent interwoven mass of long, grayish-white hairs persisting through the inflorescence; leaves glabrous on the adaxial surface, the abaxial surface arachnoid or tomentose; basal leaves 2 or 3, petioled, pinnately veined, oblong in outline, 14–16 cm. long, ca. 10 cm. wide; blades deeply pinnately lobed, the primary lobes 9 or 10, at right angles to the axis but ascending distally, extending ca. four-fifths of the distance to the midrib, each irregularly 3- to 5-lobed; petioles 5–12 cm. long, slender; cauline leaves ca. 3, the lowermost about one-half as large as the basal ones and similar; upper cauline leaves reduced and bracteiform, 4–6 cm. long, ca. 1 cm. wide; inflorescence subracemose; pedicels (2–) 4–6 cm. long; calyculate bracts 3–5, linear-subulate, 1–2 cm. long; heads 5–7, 2–2.5 cm. long; phyllaries 12 or 13, oblong or narrowly ovate, 10–12 mm. long, 3–4.5 mm. wide, densely pubescent; flowers 40 or more; corolla 11–14 mm. long, the tube 7–10 mm. long, the throat narrowly campanulate, 1–1.5 mm. long, equally broad at the apex, the lobes ca. 3 mm. long,

linear; anthers 3 mm. long; style branches 1.5 mm. long, hispid distally on the abaxial surface, the tips truncate with a terminal fringe of trichomes; mature achenes ellipsoid, obovoid or 3-angulate, 5–6 mm. long, 2–3.5 mm. wide, 1.5 mm. thick, densely villous, the hairs ascending, grayish-white or creamy, up to 1 mm. long; pappus creamy, 7–8 mm. long, clavate distally.

DISTRIBUTION: Known only from the type specimens.

This species is most unusual because of the dense, grayish-white, flocculent pubescence covering the entire plant except the adaxial surface of the leaves. The leaves are very much like those of *O. sinuatum* but the heads are much larger and the flowers have a short, but evident throat. The apparently fleshy caudex is also unique.

15. Odontotrichum platylepis (Rob. & Seat.) Rydb. Bull. Torrey Bot. Club 51: 417. 1924.

Cacalia platylepis Rob. & Seat. Proc. Amer. Acad. 28:110. 1893. Lectotype: Jalisco; Río Blanco, October 1886, *E. Palmer* 689 (GH!).

Cacalia coriacea M. E. Jones, Extracts from Contr. West. Bot. 18:80. 1933. Holotype: Jalisco; Orendain, Nov. 28, 1930, *M. E. Jones* s.n. (POM, not seen; isotype GH!).

Plants to 1.5 m. tall; stem 6–12 mm. thick at the base, densely shaggy-villous below, becoming less dense upward; leaves sparsely pubescent mostly along the veins, the abaxial surface densely pubescent; basal leaves 3 or 4, long-petioled, erect, coriaceous, broadly ovate in outline, 18–35 (–75) cm. long and broad or slightly broader; blades deeply pinnately lobed two-thirds to three-fourths the distance to the midrib, the primary lobes ca. 11, the proximal pair (6–) 10–16 (–22) cm. long, 2–6 cm. wide at the base, the distal lobes progressively smaller upward, each lobe irregularly divided into 2–4 lobes, the major secondary lobes often again lobed, the ultimate segments triangular or deltoid or oblong-obtuse, the base of the blade decurrent on the petiole for a short distance forming a leafy margin, the abaxial and adaxial surfaces very similar; petioles 16–32 cm. long, triangular in cross section, densely pubescent below becoming sparsely pubescent distally; cauline leaves several, the lowermost smaller than the basal ones but similar; upper cauline leaves bracteiform, the petiolar portion leafy-margined, clasping the stem, the blade portion sinuately lobed, the uppermost forming inflorescence bracts, the larger ones 3–6 cm. long, 1.5–4 cm. wide, distally laciniate; inflorescence corymbose, 16–27 cm. long, 16–18 cm. broad, the branches sparsely or densely arachnoid pubescent, the hairs frequently with purple crosswalls; pedicels 1.5–3 (–9) cm. long; calyculate bracts 5–8, narrowly obovate, 1.5–2 cm. long, 5–10 mm. wide, laciniate-lobed; heads 15 or fewer, 1.5–2 cm. long; phyllaries 13 or 14 (–17), narrowly ovate or elliptic, 13–15 (–16) mm. long, 4–5 mm. wide, mostly glabrous, often sparsely puberulent;

receptacle to 1 cm. across; flowers 40–80 or more per head; corolla 13–15 (–16) mm. long, the tube 10–11 mm. long, the lobes (3.5–) 4–5 (–6) mm. long, the throat none; anthers 3.5–4 mm. long; style branches 1–1.5 mm. long, the tips truncate with a subterminal fringe of trichomes; mature achenes ellipsoid, 6–7 mm. long, 3 mm. wide, 1.5–2 mm. thick, pale with ca. 10 contrasting dark ribs, the intervals between the ribs pubescent with hyaline, ascending hairs; pappus white, (8–) 10–11 mm. long, clavate distally.

DISTRIBUTION: Mostly in the central grassland regions of Jalisco around Guadalajara and extending northward to Aguascalientes. Open, rocky grasslands, scrub and pastured areas. Flowering from mid-October to December, the flowers emitting an unpleasant odor.

In the original description two specimens were cited as syntypes: Jalisco; plains of Guadalajara, Nov. 26, 1888, *C. G. Pringle* 1816 (GH!) and Jalisco; Río Blanco, October 1886, *E. Palmer* 689 (GH!). The latter was designated the lectotype because it is a more complete specimen than *Pringle* 1816. The lectotype specimen consists of a basal leaf ca. 18 cm. long, a stem in three pieces, with 6 cauline leaves below the 8-headed inflorescence (Mich. Neg. 1253). There is also a second sheet at the Gray Herbarium (an isolectotype) that has a basal leaf ca. 28 cm. long, the base of the plant with the roots, and an inflorescence with ca. 15 heads, but no portion of the stem.

This species is spectacular because of its extremely large basal leaves, more than one-half meter long, that stand erect.

AGUASCALIENTES: *McVaugh & Koelz* 48 (MICH). JALISCO: *Jones* 27692 (NY); *Palmer* 689 (US, 3 sheets, isotypes); *McVaugh* 22123 (MICH); *Pringle* 1816 (US, 2 sheets, NY, MICH, isoparatypes); *Pringle* 9873 (GH, US, NY); *Safford* 1432 (US); *Jones* s.n., Nov. 27, 1930 (GH, isotype of *C. coriacea* Jones); *Pippen* 23, 58 (MICH); *Jony* s.n., in 1892 (US).

16. Odontotrichum pringlei (S. Wats.) Rydb. Bull. Torrey Bot. Club 51: 415. 1924. PLATE 4

Cacalia cirsiifolia Hook. & Arn. Bot. Beech. Voy. 436. 1841. Holotype: Nayarit; between Tepic and San Blas, *Sinclair* s.n., in Hooker Herb. (K, not seen; Mich. Neg. 623!). Not *Odontotrichum cirsiifolium* Zucc.

Senecio cirsiifolia (Hook. & Arn.) Schultz Bip. Flora 28:499. 1845.

Cacalia pringlei S. Wats. Proc. Amer. Acad. 25:156. 1890. Lectotype: Jalisco; grassy slopes of the barranca near Guadalajara, November 1888, *C. G. Pringle* 1749 (GH!).

Plants to 1.5 m. tall; stem 4–10 mm. thick at the base, densely villous, flocculent below the lowest leaf and sparsely puberulent or becoming glabrous above; leaves sparsely pubescent with 8- to 10-celled hairs 0.3–0.5 mm. long, slightly longer and denser along the veins and on the abaxial surface; basal leaves 2–4, erect, coriaceous, long-petioled, pinnately veined, oblong or elliptic in outline, 20–35 (–40) cm. long, 13–30 cm. wide, as long as broad to twice as long as

broad; blades deeply pinnately lobed, the primary lobes 10–16, (4–) 5–10 (–15) cm. long, 3–4 cm. wide at the base, each usually divided into 3 major lobes and 2 or 3 lesser lobules or teeth, the latter usually narrowly triangular, the secondary lobes triangular or 3-angulate or again divided into 2 or 3 triangular lobules, the lobes, including the proximal pair, forming an angle with the midrib of less than 90 degrees; blades obtuse or attenuate, not cordate at the base, decurrent along the petiole for 1–2 cm. below the proximal lobes; petioles 20–30 (–40) cm. long, triangular in cross section, villous proximally, becoming sparsely pubescent distally; cauline leaves 3–7, much reduced in size, bracteiform, the lowermost leaflike, sinuately lobed, the petiole dilated at the base and clasping the stem, up to 15 cm. long, 3 cm. broad; inflorescence loosely paniculate or corymbose, 18–25 cm. long, 16–20 cm. broad, the branches subglabrous to sparsely pubescent, subtended by narrowly ovate bracts (2–) 3–5 (–7) cm. long, 0.5–1.5 cm. wide; calyculate bracts 5–8, linear-subulate, 3.5–5.5 mm. long; heads ca. 100, 10–12 mm. long; phyllaries 7 or 8 (–9), ovate or elliptic, 5–7 mm. long, 2–3 (–4) mm. wide, glabrous; receptacle 1.5–2 mm. across; flowers 11–14; corolla 6–8 (–10) mm. long, the tube 3–4 (–5) mm. long, the lobes 3–4 (–5) mm. long, linear, the median nerve strong, the throat none; anthers 2–3 mm. long; style branches 1 (–1.5) mm. long, usually hispid on the abaxial surface, the tips truncate or obtuse with a subterminal or terminal fringe of trichomes; mature achenes ellipsoid (3–) 4–5 mm. long, 2 mm. wide, 1–1.5 mm. thick, pubescent with minute, creamy or tawny hairs between the ribs, the ribs about 20, darker than the area between the ribs; pappus (4–) 6–7 mm. long, white, the tips slightly clavate; chromosome number, $n=30$ (Pippen; Turner, ined.).

Two specimens were cited in the original description as syntypes: Jalisco; grassy slopes of the barranca near Guadalajara, November 1888, *C. G. Pringle* 1749 (GH) and 1811 (GH). *Pringle* 1749 is chosen as the lectotype because it is a more complete specimen.

DISTRIBUTION: Nayarit, Jalisco, and Colima. Grasslands, pastured areas, roadsides, and less frequently rocky slopes in oak-pine woodlands. Flowering from October to early December.

This species is closely related to *O. platylepis* and *O. sinuatum*, differing from the former in having smaller heads; from the latter in having pubescent achenes and differently shaped leaves. *Cacalia cirsiifolia* Hook. & Arn., known only from the very incomplete type specimen consisting of just a portion of the inflorescence and one upper cauline leaf, is undoubtedly conspecific with *O. pringlei* because of the similarity of the heads and the pubescent achenes.

COLIMA: *Palmer* 1234 (GH, NY, US). JALISCO: *McVaugh & Koelz* 1253, 1104 (MICH); *McVaugh* 13616, 21765* (MICH); *Pippen* 37*, 41, 59 (MICH); *Pringle*

1811 (US, isoparatype of *C. pringlei* S. Wats.); *Pringle* 11499 (GH, MICH, US). NAYARIT: *Ferris* 5881 (US); *Mexia* 845 (GH, US); *McVaugh & Koelz* 601 (MICH); *Palmer* s.n., Jan. 5–Feb. 6, 1892 (US); *Barclay* s.n. (GH, probably collected in late December 1837 at the same time and place as the type of *Cacalia cirsiifolia* Hook. & Arn., since Barclay and Sinclair were together at that time, attached to the H.M.S. *Sulphur* [McVaugh, manuscript ined.]).

17. Odontotrichum purpusii (Greenm.) Rydb. Bull. Torrey Bot. Club 51:418. 1924.

Cacalia purpusii Greenm. Univ. Calif. Publ. Bot. 4:95. 1910. Holotype: Puebla; Cacalote, August 1909, *C. A. Purpus* 3845 (F!, isotype NY!).

Plants to 0.6 m. tall, pubescent with white, stiff, multicellular hairs; stem slender, ca. 3 mm. thick at the base; basal leaves 2–4, pinnately veined, petioled, subcoriaceous, ovate or broadly elliptic, to 8 cm. long, 6 cm. wide, the margin of the blade doubly dentate with two alternating series of large and small teeth, respectively, the base of the blade truncate or obtuse; petioles terete, 3–9 cm. long, about as long as the blade; cauline leaves ca. 4, the lowermost smaller than the basal ones but similar to them; upper cauline leaves reduced, bracteiform; inflorescence compact or spreading, corymbose, 3–14 cm. long, 3–19 cm. broad, the branches arachnoid-pubescent or tomentose, subtended by linear-subulate bracts ca. 5 mm. long; calyculate bracts 3–7, linear-subulate, 3–4 mm. long; heads 15–30, 10–12 mm. long; phyllaries 7 or 8, oblong or ovate, 5.5–7 mm. long, 1.5–2 mm. wide, glabrous; flowers 10–13, corolla ca. 7 mm. long, the tube (3.5–) 4 mm. long, the lobes (3–) 3.5 mm. long; anthers 2.5 mm. long; style branches 1.5 mm. long, the tips truncate with a terminal fringe of trichomes; mature achenes oblong, ca. 3.5 mm. long, 1 mm. wide, glabrous, brown; pappus 4–6 mm. long, creamy or tawny.

DISTRIBUTION: Puebla and Oaxaca. Known only from three collections. Flowering in June to August.

This taxon is quite closely related to the *O. silphiifolium-goldsmithii* group but is much smaller and does not occur within the present known geographical range of either of the others. When more material of this taxon becomes available and can be studied it may indicate that *O. purpusii* should not be considered as a distinct species. It is considered distinct here because of the general small habit, distinct geographical distribution, and lack of correlative evidence to combine it with any other taxon.

OAXACA: *Conzatti* 4015 (US); *Conzatti & Gonzales* 1237 (GH, this specimen has no leaves).

18. Odontotrichum radulifolium ["radulaefolium"] (H.B.K.) Rydb. Bull. Torrey Bot. Club 51:415. 1924.

Cacalia radulifolia ["radulaefolia"] H.B.K. Nov. Gen. et Sp. 4:169. 1820. (Folio ed. 4:132. 1820). Holotype: Guanajuato; between the village of Temascatio and Guanajuato, no date, 1050 hex., *Humboldt & Bonpland* s.n. (P, not seen; Field Mus. Neg. 37875!).

Senecio radulaefolius (H.B.K.) Schultz Bip. Flora 28:498. 1845.
Cacalia schaffneri A. Gray, Proc. Amer. Acad. 19:53. 1883. Lectotype: near San Luis Potosí in 1876, *Schaffner* 294 (GH!).
Odontotrichum schaffneri (A. Gray) Rydb. Bull. Torrey Bot. Club 51:415. 1924.

Plants to 1.5 m. tall; entire plant pubescent except the phyllaries, the hairs white, 5- to 7-celled; stem 3–5 (–8) mm. thick at the base, green or purplish; basal leaves 2 or 3, long-petioled, pinnately veined, ovate-cordate or subcircular in outline, (6–) 10–12 (–18) cm. long, (8–) 12–14 (–22) cm. wide, usually 3–5 cm. broader than long or as long as broad, subpeltate, the petiole attached to the blade 2–10 (–30) mm. above the base; blades pinnately lobed three-fifths to four-fifths the distance to the midrib, the primary lobes 7–9 (–11), each divided into usually 3 (2–5) lobes, the secondary lobes often lobed, 3-angulate or coarsely dentate, the lowermost pair of primary lobes deflected, parallel to the petiole; petioles (7–) 12–21 (–30) cm. long; cauline leaves 2–4, the lowermost about as large as the basal ones and similar, but the base of the petiole more dilated and often leafy-margined; upper cauline leaves progressively smaller upward, bracteiform, auriculate-based, elliptic or ovate, distally sinuately 7- to 9-lobed; inflorescence loosely corymbose, (3–) 12–30 cm. long and broad, the branches subtended by linear-subulate bracts (5–) 7–10 mm. long; calyculate bracts 3–5, subulate, 2–5 mm. long; heads (25–) 50–75, 10–11 mm. long; phyllaries 5, oblong or narrowly ovate, 5–7 mm. long, 1–2 (–3) mm. wide, glabrous; flowers 5 or 6; corolla 6.5–7.5 mm. long, the tube 3–3.5 (–4) mm. long, the throat very short, ampliate, 0.5–0.7 mm. long, 0.7–1 mm. wide at the apex, the lobes 3–3.5 mm. long; anthers 2–3 mm. long; style branches 1–1.5 mm. long, hispid on the abaxial surface, the tips truncate or obtuse with a subterminal fringe of trichomes; mature achenes ellipsoid, 4 mm. long, 1.5 mm. wide, brown, ca. 14-ribbed, pubescent, the hairs 0.5 mm. long, greenish or tawny; pappus creamy or fuscous, 4–5.5 mm. long.

DISTRIBUTION: Sinaloa, Durango, San Luis Potosí and Guanajuato to Tamaulipas. Grassy openings in oak-pine woodlands and pastures. Flowering in July and August.

Comparison of the type specimen of *Cacalia schaffneri* A. Gray with the photograph of the type of *C. radulifolia* H.B.K. and the similarity of the original descriptions of these two taxa indicate that they are conspecific, even though the subpeltate condition of the leaves was not mentioned in the original description of *C. radulifolia*. Gray mentioned in his description of *C. schaffneri* that possibly this was the little known *C. radulifolia* of H.B.K. This is the only species of *Odontotrichum* with subpeltate leaves.

DURANGO: *Graham* 100 (MICH); *Feddema* 1821 (MICH); *Maysilles* 7587 (MICH). GUANAJUATO: *Kenoyer* 2110, 2300 (GH); *Schumann* 148 (US). SAN

Luis Potosí: *Manning & Manning* 53560 (GH); *Mickel* 501, 561 (MICH); *Parry & Palmer* 543 (NY); *Pringle* 3566 (GH, US); *Pringle* 4095 (NY, US); *Schaffner* 294 (NY, US, isotype of *C. schaffneri* A. Gray; the US specimen also bears the number 724 assigned to the sheet by A. Vigener who purchased many of the Schaffner collections [J. Rzedowski, pers. comm.]). Sinaloa: *Powell & Edmondson* 929 (MICH, TEX). Nuevo Leon: *Meyer & Rogers* 2608 (MICH) Tamaulipas: *Stanford, Retherford & Northcraft* 818 (GH); *Stanford, Taylor, & Lauber* 2421 (MICH, NY, TEX, US).

19. Odontotrichum silphiifolium (Rob. & Greenm.) Rydb. Bull. Torrey Bot. Club 51:416. 1924.

Cacalia silphiifolia Rob. & Greenm. Amer. Journ. Sci. III. 50:158. 1895. Holotype: México; Sierra de las Cruces, Aug. 21, 1892, *C. G. Pringle* 5251 (GH!).

Plants to ca. 1.5 m. tall; roots exuding an amber-colored fluid when cut; stem 1–1.5 cm. thick at the base, subglabrous or puberulent upward; leaves minutely puberulent especially along the veins; basal leaves 2 or 3, erect, long-petioled, pinnately veined, ovate-cordate, (13–) 15–20 (–45) cm. long from the tip to the basal sinus, (11–) 14–21 cm. wide, usually 2–4 cm. longer than wide, occasionally as wide as long; blades sinuately double-dentate, the teeth in two alternating series of large and small, respectively, the base of the blade cordate or sagittate, rarely truncate, the basal lobes 4–7 cm. long, 5–9 cm. wide, rounded; petioles (15–) 20–30 cm. long; cauline leaves 2–4, the lowermost similar to the basal ones but smaller, occasionally deltoid and truncate-based with the petiolar portion broadly leafy-margined, auriculate-based and clasping the stem; upper cauline leaves smaller, bracteiform; inflorescence tightly corymbose, usually 6–11 cm. long and broad, occasionally up to 28 cm. long, ca. 20 cm. broad, the branches tomentose, subtended by linear or narrowly ovate bracts 1.5 cm. long, 1 mm. wide; pedicels 0.3–3 cm. long; calyculate bracts 1–5, linear-subulate, (3.5–) 5–7 mm. long; heads 50–75; 10–15 mm. long; phyllaries 8, narrowly ovate or ovate, (6–) 7–8 mm. long, 1.5–2 (–3) mm. wide, glabrous; flowers 9–13; corolla 8.5–9 (–11) mm. long, the tube 5 (–6) mm. long, the lobes 3.5–4 (–5) mm. long, the throat none; anthers 2–3 mm. long; style branches 1–1.5 mm. long, the tips truncate with a sparse terminal fringe of trichomes; mature achenes ellipsoid, 4–5.5 mm. long, 1.5–2 mm. wide, 1–1.5 mm. thick, glabrous, light brown, inconspicuously 16- to 18-ribbed; pappus creamy, (5–) 7–8 mm. long.

Distribution: Michoacán, east to México and Hidalgo, south to Morelos. Grasslands, pastures, borders, and openings in oak woodlands. Flowering in August and September.

This species is very closely related to *O. goldsmithii* and may be distinguished from it by its coarser habit, larger, puberulent, cordate leaves and more compact, tight inflorescence with larger heads.

DISTRITO FEDERAL: *Matuda* 19184 (US). HIDALGO: *Rose et al.* 9187 (GH, NY, US). MÉXICO: *Matuda* 19417 (NY); Pringle 6453 (GH, MICH, NY, US). MICHOACÁN: *King* 3615 (MICH, NY, TEX, US); *Pippen* 54 (MICH). MORELOS: *Moore* 3421 (GH); *Orcutt* 3746 (GH, US); *Rose & Hay* 5311 (GH, US); *Pringle* 9080 (GH, US).

20. Odontotrichum sinuatum (Cerv.) Rydb. Bull. Torrey Bot. Club 51:415. 1924.

Cacalia sinuata Cerv. *in* Llave & Lex. Nov. Veg. Desc. fac. 1:29. 1824. Holotype: Distrito Federal; mountains of the desert of San Angel, near Mexico City, *Cervantes* s.n. (not seen).

Senecio albo-lutescens Schultz Bip. Flora 28:498. 1845. Based on *Cacalia sinuata* Cerv. not *S. sinuatus* H.B.K.

Senecio calophyllus Hemsl. Biol. Centr. Amer. Bot. 2:237. 1881. Name illegitimate.

Slender plants to 1.5 (–2) m. tall; stem 4–6 mm. thick at the base, light green, pubescent below becoming subglabrous above; leaves sparsely puberulent, mostly along the veins and margins; basal leaves 3–5 (–7), erect, long-petioled, oblong-cordate in outline, (8–) 12–19 cm. long, (8–) 12–17 cm. wide, usually 2–3 cm. longer than broad or as long as broad; blades deeply lobed to within 1–3 cm. of the midrib, the primary lobes 8–11 (–13), 1–3 cm. broad at the base, mostly at right angles to the midrib, each lobe distally divided into 3 major secondary lobes and 2 or 3 lesser lobules or coarse teeth, the proximal pair of primary lobes usually deflected, more or less parallel to the petiole; petioles 10–40 cm. long, usually longer than the blade, slender, glabrous, green, often mottled with purple; cauline leaves 3–5 or more, the lowermost similar to the basal ones and about one-third as large, the petiole more clasping at the base; upper cauline leaves greatly reduced, bracteiform, the petiolar portion leafy-margined and clasping the stem, distally lobed; inflorescence corymbose (10–) 15–27 cm. long, (6–) 12–21 cm. broad, the branches sparsely to arachnoid-pubescent, subtended by narrowly ovate bracts 1–1.5 cm. long, 3 mm. wide, occasionally larger; pedicels 3–5 mm. long; calyculate bracts 3–7, linear-subulate, 3–7 mm. long; heads 75–100, 10–12 mm. long; phyllaries mostly 8 (7–9), elliptic or narrowly ovate, 5–6 (–7) mm. long, 2–3 mm. wide, glabrous, receptacle often slightly pubescent, up to 2 mm. across; flowers (9–) 10–11 (–13); corolla 6–7 mm. long, the tube 3–3.5 (–4) mm. long, the lobes 3–3.5 mm. long with a strong median nerve; anthers 2–3 mm. long; style branches 1–1.5 mm. long, the tips truncate with a terminal fringe of trichomes; mature achenes ellipsoid, 3.5–4 mm. long, 1.5–2 mm. wide, ca. 1–1.5 mm. thick, glabrous, light brown, ca. 20–striated; pappus white, 4–5.5 (–7) mm. long; chromosome number, $n=30$ (Turner, ined.).

DISTRIBUTION: From southern Chihuahua south and east to México. Common in grasslands, pastures, and borders of oak-pine

woodlands, occasionally in poorly drained areas. Flowering from August to October.

This is one of the most common species in western and central Mexico and exhibits considerable morphological variation. The basal leaves on the same plant as well as within the same population may vary in size, shape, and depth of lobing.

The holotype of this species has not been located. McVaugh and Rzedowski searched in Mexico City and McVaugh in Madrid but no Cervantes specimen was located. It is possible that no type specimen exists, as few other La Llave and Lexanza specimens are known. The original description, however, is sufficiently diagnostic to accept this name.

AGUASCALIENTES: *McVaugh & Koelz* 49 (MICH); *Pippen* 1, 7 (MICH). DISTRITO FEDERAL: *Bourgeau* 716 (GH, US); *Smyth* 172 (US). DURANGO: *Gould* 8989 (MICH); *King* 3734 (NY, TEX); *McVaugh* 21733 (MICH, part of hybird population between *O. sinuatum* and *O. globosum*); *Maysilles* 7572, 7793, 7880, 8448, (MICH), 8485 (MICH, NY); *Palmer* 651 (GH, NY, US); *Powell & Edmondson* 948 (TEX); *Gentry* 8562 (MICH). GUANAJUATO: *Duges* 451 (GH). JALISCO: *Hartweg* 125 (GH, NY); *McVaugh* 12810 (MICH); *McVaugh & Koelz* 276 (MICH); *Pippen* 9*, 22, 57 (MICH). MÉXICO: *Matuda* 19706, 21808, 26882 (NY); *Pippen* 56 (MICH); *Pringle* 4272, 9875 (GH, NY, US); *Rose & Painter* 7808 (GH, US). MICHOACÁN: *Arsène* 5740 (US); *Feddema* 10 (MICH); *Pippen* 45, 50 (MICH). PUEBLA: *Arsène* 93A, 334, 93, 1181 (US). WITHOUT LOCALITY: *Vischer* 58 (NY).

21. Odontotrichum tussilaginoides (H.B.K.) Rydb. Bull. Torrey Bot. Club 51:416. 1924.

Cacalia tussilaginoides H.B.K. Nov. Gen. et Sp. 4:168. 1820. (Folio ed. 4:132. 1820.) Holotype: Hidalgo; Real del Monte, 1420 hex., no date, *Humboldt & Bonpland* s.n. (P, not seen; Field Mus. Neg. 37878!).

Senecio tussilaginoides (H.B.K.) Schultz Bip. Flora 28:498. 1845. Not *S. tussilaginoides* Walt. 1788.

Senecio farfarus Hemsl. Biol. Centr. Amer. Bot. 2:239. 1881. Based on *Cacalia tussilaginoides* H.B.K., not *S. tussilaginoides* Walt. 1788.

Cacalia ampullacea Greenm. Proc. Amer. Acad. 34:577. 1899. Holotype: Hidalgo; Sierra de Pachuca, 9,000 ft., July 17, 1898, *C. G. Pringle* 1617 (GH!).

Odontotrichum ampullaceum (Greenm.) Rydb. Bull. Torrey Bot. Club 51:416. 1924.

Roots and lower portion of the stem not seen; erect herbs up to 1.3 m. tall (acc. *Balls* 5428); stem pubescent; leaves puberulent on the adaxial surface, the abaxial surface gray-tomentulose, the tomentum often flocculent; basal leaves presumably 2 or more, pinnately veined, ovate-cordate in outline, 20–30 (–35) cm. long from the apex to the basal sinus, 17–35 cm. wide, usually 2–4 cm. longer than broad or occasionally as broad as long; blades lobed one-half the distance to the midrib (at least on the distal portion of the blade), the primary lobes 10–12, 5–6 (–14) cm. long, 4–5 (–11) cm. broad at the

base, each sinuately and irregularly divided into at least 3 lobes, the secondary lobes usually coarsely dentate; petioles at least as long as the blades, usually longer (to 0.5 m.); lower cauline leaves not seen; upper cauline leaves leafy, bracteiform, ovate, naviculate, clasping the stem, 11–20 cm. long, 10–12 cm. wide, the margin toothed or sinuately lobed; inflorescence tightly corymbose, 17 (–21) cm. long, 12–17 cm. broad, the branches tomentose, the lowermost branches in the axils of the uppermost leaves, the distal branches subtended by linear-subulate bracts 1.5–4 cm. long, 1–2 (–4) mm. wide; calyculate bracts 4 or 5, linear-subulate, 3–5 mm. long; heads 100 or more, 7–10 mm. long; phyllaries 5, narrowly ovate, 5–7 mm. long, 1.5–2 (–3) wide, glabrous, often purplish; flowers 5 or 6, corolla 6–7 mm. long, the tube 3–3.5 mm. long, the lobes 3–3.5 mm. long, the throat none; anthers 2 (–2.5) mm. long; style branches 1 mm. long, hispid on the abaxial surface, the tips truncate or obtuse with a subterminal fringe of trichomes; mature achenes not seen, immature achenes 3.5–4 mm. long, pale tan, densely pubescent; pappus creamy or tawny, 4–5 (–7) mm. long.

DISTRIBUTION: Known only from Hidalgo and Veracruz. In wet mountain meadows. Flowering in August (?) (Kunth stated in the description that the plants flowered in May. The specimens I have examined flowered in August). This is one of the few species of *Odontotrichum* found in eastern Mexico.

This species is somewhat similar to *O. amplifolium*, differing mostly in the smaller heads with fewer flowers and the pubescent achenes. Comparison of the description and type specimen of *Cacalia ampullacea* Greenm. with the description and type photograph of *O. tussilaginoides* indicates that they are conspecific because of their similarity in appearance and their many common characters. Greenman apparently reached this conclusion after the publication of *C. ampullacea* because the type specimen is annotated as *C. tussilaginoides* H.B.K., in what appears to be Greenman's writing.

HIDALGO: *Rose & Hay* 5574 (US); *Rose & Painter* 6738 (GH, US); *Pringle* 9868 (GH, NY, US). VERACRUZ: *Balls* 5428 (US).

3. Pericalia

Pericalia (Cass. Dict. Sci. Nat. 48: 459. 1827, not validly published) Rydb. Bull. Torrey Bot. Club 51: 376. 1924.

Perennial, leafy-stemmed herbs, 1.5–2 m. tall; roots fibrous, fleshy; stems usually solitary, erect, annual, terete to often 6- to 8-angulate distally, pubescent or glabrous, tuberculate at base, the clustered subterranean tubercles each up to 2.5 cm. thick, 5 cm. long, pubescent with minute, multicellular, tan hairs; leaves cauline, not forming a basal rosette, succulent when fresh, coriaceous when dry, petiolate or

sessile, alternate, clustered toward the middle of the stem but continuing upward to the inflorescence, becoming smaller and widely separated distally, not usually becoming bracteiform; inflorescence paniculate or corymbose; heads usually few, nodding, 15–20 mm. long, subtended by 10–15, linear or narrowly triangular, calyculate bracts as long as or longer than the phyllaries and loosely surrounding them, especially in bud; involucre campanulate to turbinate, the phyllaries subequal, biseriate appearing uniseriate, imbricate, the overlapped margins subscarious, the exposed surfaces glabrous, the tips fringed with minute trichomes up to 0.3 mm. long; receptacle flat or nearly so, alveolate, not paleaceous; flowers all discoid, perfect, fertile, 25–50 or more per head; corollas glabrous, creamy or nearly white but never yellow, the tube narrowly cylindrical, ca. 0.5 mm. in diameter, the limb divided into 5, equal, narrowly triangular, 3-nerved, recurved lobes connate into a campanulate throat, 2–5 mm. long, as long as or twice as long as the lobes; anthers 3–4 mm. long, exserted beyond the corolla throat, the bases rounded or slightly sagittate, the terminal appendages trullate, rounded or ovate, 0.5–0.7 mm. long; style branches 1–2 mm. long, slightly flattened, recurved, the stigmatic area covering most of the adaxial surface, the abaxial surface glabrous or hispidulous below, the unappendaged tips truncate, to obtuse, fringed with nonglandular "pollen-producing" trichomes; achenes narrowly cylindrical, subterete in cross section, glabrous, purplish brown, 10-ribbed; pappus creamy or white, distally clavate.

TYPE SPECIES: *Pericalia sessilifolia* (Hook & Arn.) Rydb.

Cassini suggested that *Cacalia cordifolia* H.B.K. should be considered as either a separate genus or subgenus under the name *Pericalia* but he did not validly publish the name as either. DeCandolle cited *Pericalia* as a synonym of *C. cordifolia* H.B.K. and Rydberg used *Pericalia* as a genus in 1924.

Microscopic examination of freehand sections of the unique tubercles revealed their stemlike nature by the presence of discrete collateral vascular bundles. The parenchyma cells contain needle-shaped crystals. The tubercles function not only in storage but also in vegetative reproduction, since in some circumstances they give rise to new flowering stems.

Key to Species of *Pericalia*

1. Flowers 40–50 per head; lobes of the corolla as long as the throat, 2–3 mm. long; leaves broadly ovate or elliptic, the margin coarsely toothed or lobulate, the lobules broader than long . . . . . **2. P. sessilifolia**
1. Flowers 25–35 per head; lobes of the corolla less than half as long as the throat, 1–1.5 mm. long, the throat 4–5 mm. long; leaves deltoid or subcircular, 3- to 7-lobed, the lobes longer than broad . . . . . **1. P. michoacana**

266-836—68——4

1. Pericalia michoacana (B. L. Rob.) Rydb. Bull. Torrey Bot. Club 51:377. 1924. PLATE 5

Cacalia michoacana B. L. Rob. Proc. Amer. Acad. 43:46. 1907. Holotype: Michoacán; Uruapan, on pine covered crater cone, 1,680 m., Oct. 31, 1905, *C. G. Pringle* 10117 (GH!).

Cacalia trigonophylla S. F. Blake, Journ. Wash. Acad. 19:280. 1929. Holotype: Jalisco; San Sebastian, trail to mine La Sabala, Feb. 10, 1927, *Ynex Mexia* 1656 (US!).

Slender herbs 0.6–1.5 (–2) m. tall; underground tubercles 1.5–2.5 cm. thick, to 5 cm. long; stem 2–5 (–7) mm. thick at the base, greenish, often mottled with purple, glabrous to sparsely or densely pubescent proximally, becoming glabrous and often glaucous above; leaves 10–15 or more, long-petioled, subpalmately veined with 3–5 principal veins with the central vein stronger, densely to sparsely pubescent to glabrous; blades variable in shape from subcircular-cordate-based with 5–7 deltoid or triangular lobes, to broadly deltoid-hastate with 3 major, narrowly triangular lobes, 4–7 (–10) cm. long from the basal sinus to the tip, 5.5–10 (–16) cm. wide, usually 2–3 cm. wider than long, progressively smaller upward, the margins minutely or coarsely dentate; petioles 5–10 (–15) mm. long, purplish; inflorescence racemose or paniculate, 10–20 cm. long, 8–12 cm. broad or larger, the distal branches subtended by linear-subulate bracts 1–1.5 cm. long, the proximal branches often in the axils of the uppermost leaves; pedicels 2–5 (–7) cm. long; calyculate bracts 10–15, linear or narrowly triangular, 4–5 (–7) mm. long; heads mostly 6–12 (–50), nodding, 15–20 mm. long; phyllaries (10–) 12 or 13, narrowly ovate or narrowly oblong, (7–) 10–13 mm. long, 1–2 mm. wide; receptacle 4–5 mm. across; flowers 25–35; corolla 9–12.5 mm. long, the tube (3.5–) 4–4.5 (–5.5) mm. long, the throat funnelform or campanulate, 4–5.5 mm. long, 1.5 mm. wide at the apex, the lobes 1–1.5 mm. long, triangular, strongly recurved; anthers 3.5–4 mm. long; style branches ca. 1.5 mm. long, the tips truncate or rounded with a sparse subterminal fringe of trichomes; achenes narrowly oblong or narrowly obovoid, terete in cross section, 2.5 mm. long, 0.5 mm. thick, glabrous, dark brown with 10 pale ribs; pappus (8–) 9–10 (–11) mm. long, white, slightly clavate distally; chromosome number, $n=30$ (Pippen).

DISTRIBUTION: From northwest Jalisco eastward to México. Growing mostly on rocky slopes in oak-pine woods. Flowering in November and December.

The specimens examined show a wide range of variation in leaf shape and pubescence between the two extreme forms described above. Some correlation between leaf shape and pubescence is apparent since the plants with 5- to 7-lobed leaves tend to be more pubescent and those plants with 3-lobed leaves tend to be glabrous and glaucous. A specimen from eastern Jalisco (*McVaugh & Koelz* 435) has more

rounded lobes than the other specimens. Despite these variations all of these specimens form only one taxon.

Comparison of the types of *Pericalia michoacana* and *Cacalia trigonophylla* and examination of a large sample of these taxa indicate that they are conspecific. They have the same number of phyllaries and flowers in a head and the morphological structure of the flowers is the same. The only observable difference is in the pubescence and the number of lobes. Blake based *C. trigonophylla* on a collection in which the leaves were 3-lobed and subglabrous. No geographical or ecological differences are noticed between these two extremes in vegetative form and therefore no nomenclatural status is given to these variations.

JALISCO: *Mexia* 1656 (US, MICH, isotypes of *C. trigonophylla* Blake); *McVaugh* 14290, 21355, 14136, 14093, 22071 (MICH); *Pippen* 26, 38, 63*, 65* (MICH); *McVaugh & Koelz* 435 (MICH). MÉXICO: *Hinton et al.* 2755 (US), 4993 (NY, US); *Moore & Cetto* 5469 (MICH). MICHOACÁN: *Hinton et al* 12718, 13469 (MICH, NY); *Pringle* 10117 (US, isotype).

2. Pericalia sessilifolia (Hook. & Arn.) Rydb. Bull. Torrey Bot. Club 51:376. 1924.

Cacalia cordifolia H.B.K. Nov. Gen. et Sp. 4:168. t. 360. 1820. Holotype: México; Santa Rosa, *Humboldt & Bonpland* s.n. (P, not seen; Field Mus. Neg. 37865!), not *Cacalia cordifolia* L.f.

Cacalia sessilifolia Hook. & Arn. Bot. Beech. Voy. 436. 1841. Holotype: Nayarit; between San Blas and Tepic, in 1837, *Sinclair* s.n. in Hooker Herb. (K, not seen; MICH Neg. 621!).

Senecio ovatifolius Schultz Bip. Flora 28:498. 1845. Based on *Cacalia cordifolia* H.B.K. not *S. cordifolius* L.f.

Senecio beecheyanus Schultz Bip. Flora 28:499. 1845. Based on *Cacalia sessilifolia* Hook. & Arn. Name illegitimate.

Senecio cardiophyllus Hemsl. Biol. Centr. Amer. Bot. 2:237. 1881. Based on *Cacalia cordifolia* H.B.K. Name illegitimate.

Senecio sessilifolius (Hook. & Arn.) Hemsl. Biol. Centr. Amer. Bot. 2:247. 1881. Based on *Cacalia sessilifolia* Hook. & Arn.

Cacalia nutans Sessé & Moc. Pl. N. Hisp. ed. 1. 132. (Fl. Mex. ic. ined. 145; Field Mus. Neg. 30705!) 1889. Lectotype: Without locality (presumably "in humidis unbrosisque Tepalpae circuitibus prope Mexicanum"), *Sessé & Moc.* 1488 or 2822! (both numbers appear on the specimen), Field Mus. Neg. 42285.

Pericalia ovatifolia (Schultz Bip.) Rydb. Bull. Torrey Bot. Club 51:377. 1924.

Plants 0.5–1.5 (–1.8 m., *Balls* 5575) m. tall; tubercles 2–2.5 cm. thick, to 5 cm. long; entire plant glabrous and glaucous, often sparsely pubescent when young; stems 3–9 mm. thick at the base; leaves 10–15, petiolate or sessile, subpalmately veined with often 3 principal veins, the central one usually dominant; blades cordate-based, broadly ovate or broadly elliptic, the larger ones 4–13 cm. long from the basal sinus to the apex, 5–12 (–14) cm. wide, usually 1–3 cm. wider than long (often as long as wide to 1½ times longer than wide), the margin

variable from subentire to dentate to 9- to 14-lobulate, the lobules, when present, usually broader than long; petioles (when present) subterete, purplish green, 3–9 cm. long; inflorescence corymbose or paniculate, 10–30 cm. long, 7–18 cm. broad, the proximal branches often in the axils of the distal leaves, the other branches subtended by subulate or narrowly ovate bracts 7–10 mm. long, 1 mm. wide; pedicels (2–) 3–6 (–9) cm. long; calyculate bracts 10–16, linear or narrowly triangular, 6–11 mm. long; heads 6–15 (–20), 15–20 mm. long; phyllaries 12–14 (–15), narrowly ovate or narrowly triangular, (9–) 11–14 mm. long, 2–3 mm. wide, greenish or purplish; receptacle ca. 7 mm. across; flowers 40–50 or more; corolla (7–) 8–12 (–13) mm. long, the tube (3.5) 4–5 (–7) mm. long, the throat 2–3 mm. long, 1–1.5 mm. across at the top, the lobes about as long as the throat, 1.5–3 mm. long, strongly recurved; anthers 3–3.5 (–4) mm. long; style branches 1–1.5 (–2) mm. long, recurved; mature achenes oblong or ellipsoid, subterete in cross section, 3.5 mm. long, 1–1.5 mm. wide, ca. 0.5–1 mm. thick, glabrous, purplish brown, 10-ribbed; pappus white (7–) 8–10 mm. long, distally clavate; chromosome number, $n=30$ (Pippen).

DISTRIBUTION: Durango, Nayarit, and Jalisco, east to Michoacán and México. Common on rocky slopes in the oak-pine woodlands. Flowering in September and October.

Comparison of *Cacalia cordifolia* H.B.K. and *P. sessilifolia* (Hook. & Arn.) Rydb. indicate that they are conspecific. They differ only in the presence or absence of the petiole. Several specimens from Nayarit have both sessile and petiolate leaves on the same plant. The heads, flowers, and other morphological characters are similar. The sessile-leaved plants are apparently vegetative variations that occur several times within the range of the petiolate forms. This difference is not significant enough for nomenclatural status.

This species is a victim of nomenclatural rules. Since *Cacalia cordifolia* H.B.K. was superfluous when published because of the earlier *C. cordifolia* L. f., a different taxon, the next oldest valid name for this taxon is *Cacalia sessilifolia* [*Pericalia sessilifolia* (Hook. & Arn.) Rydb.]. This is unfortunate since the petiolate-leaved plants are by far more common than the sessile-leaved forms.

AUGUASCALIENTES: *McVaugh & Koelz* 147 (MICH); *Pippen* 5 (MICH). DISTRITO FEDERAL: *Balls* 5575 (US); *Bourgeau* 715 (GH); *Pringle* 7983 (GH); *Lyonnet* 194 (GH, NY, US); *Purpus* 5625 (GH, NY, US). DURANGO: *Gentry* 6968 (GH, MICH, US); *McVaugh* 21658 (MICH); *Maysilles* 7579 (MICH); *Pennell* 18345 (NY, all of the specimens from Durango are of slightly smaller stature with more, smaller leaves). GUANAJUATO: *Duges* 481 (GH, US). JALISCO: *McVaugh* 13559, 13625, 17118, 17183, 18121 (MICH); *McVaugh & Koelz* 920 (MICH); *Mexia* 1450 (US); *Palmer* 576 (GH, NY, US); *Pippen* 17, 18, 31, 33, 34, 61*, 64 (MICH); *Pringle* 1736 (GH, MICH, NY, US), 9869 (GH, NY, US), 11497 (GH, MICH, US); *Safford* 1451 (US); *Rose* 2828 (GH, US). MÉXICO: *Matuda* 21825

(NY). MICHOACÁN: *Arsène* s.n., Sept. 11, 1909, Sept. 14, 1911, 5729, 7347 (US); *Feddema* 161 (MICH); *Pippen* 51 (MICH). NAYARIT: *Feddema* 381, 1345 (MICH): *McVaugh & Koelz* 479, 792, 656 (MICH); *Mexia* 635 (US); *Ortega* 5727 (US); *Palmer* 1832 (GH, NY, US); *Pippen* 13, 15 (MICH). QUERETARO: *Matuda* 29787 (NY). SAN LUIS POTOSÍ: *Palmer* 47 (GH, NY, US); *Parry & Palmer* 541 (GH, US); *Schaffner* 255, 33 or 37? (GH).

Three specimens in the herbarium at the University of Michigan do not fit precisely into either of the above taxa, *P. sessilifolia* or *P. michoacana*. Two of these, *McVaugh* 13469 and 13825 (from northeast slopes of the Nevado de Colima, below Canoa de Leoncito, 2,250–2,550 m.), have leaves similar to *P. michoacana* in that they are subcircular, 7-lobed, and pubescent, but they are about 0.5 times larger with much longer petioles and the inflorescence has larger heads with more flowers. The phyllaries are finely pubescent with fuscous hairs and the heads are subtended by about 15 calyculate bracts as wide as but longer than the phyllaries.

These specimens may represent a different species but, because of the paucity of material available and its rather close similarity to *P. michoacana*, I will only mention their existence for the present.

The third nonconforming specimen, *McVaugh* 13862 (Sierra de Manantlán, 15–20 miles southeast of Autlán, near Asseradero El Cuartón, 2,500 m.), differs from the above in that the leaves are less deeply lobed, less pubescent, and the trichomes are mostly restricted to the leaf margins; the phyllaries are glabrous, the subinvolucral bracts no longer than the phyllaries and somewhat narrower. This specimen approaches *P. sessilifolia* but differs in the longer petioles, the more subcircular than ovate, 7-lobed leaves, and the presence of pubescence. Future collections and field observations in this region will be necessary to properly interpret this specimen.

4. Psacalium

Psacalium Cass. Dist. Sci. Nat. 43:461. 1826.

Perennial, subscapose herbs, 0.1–3 m. tall; roots fleshy, fibrous; caudex tough, to 5 cm. long, 3 cm. thick, the nodes and terminal buds densely covered with masses of tawny, multicellular hairs, 1–2 cm. long; stems usually solitary, annual, erect, slender or stout, usually terete, glabrous or pubescent; radical leaves forming a basal rosette of two to several, centrally peltate with several principal radiating veins, each pinnately subdivided, the blades variously lobed, rarely subentire, mostly pubescent; cauline leaves alternate, progressively smaller upward, the uppermost bracteiform, usually nonpeltate with a broad leafy-margined petiole and palmately 3- to 7-lobed blade; inflorescence paniculate or corymbose, the branches often stipitate glandular, with minute, multicellular glands, 0.5 mm.

long, subtended by small, linear-subulate or large, leafy, often vaginate bracts; heads few to many, calyculate, the bracts 3–5, as long as the phyllaries or shorter (longer in *P. peltatum*); involucre campanulate, turbinate or less frequently cylindrical, the phyllaries 5–17, subequal, biseriate appearing uniseriate, the overlapped margins subscarious, the exposed surfaces pubescent or glabrous, the tips fringed with minute trichomes up to 0.3 mm. long; receptacle flat or nearly so, alveolate, not paleaceous, occasionally sparsely pubescent; flowers all discoid, fertile, 5–80 per head; corollas glabrous, creamy or nearly white, occasionally greenish or purplish tinted but never yellow, the tube narrowly cylindrical, 0.5 mm. in diameter, the limb divided into 5, equal, narrowly-triangular, 3-nerved, ascending or spreading, not recurved lobes, connate into a short, ampliate or campanulate throat, about 1 mm. long, 1–1.5 mm. wide (or occasionally lacking), the lobes longer than the throat and as long as to one-half as long as the tube; anthers 2–4 mm. long, exserted beyond the corolla throat, rounded or slightly sagittate at the base, the terminal appendages trullate or ovate 0.5–0.7 mm. long; style branches 0.7–2 mm. long, slightly flattened, recurved or spreading, the stigmatic surface covering most of the adaxial surface, the abaxial surface glabrous or hispidulous below, the unappendaged tips truncate to obtuse with a fringe of nonglandular "pollen producing" trichomes; achenes obovoid or ellipsoid, somewhat compressed and elliptic or broadly elliptic in cross section, glabrous or pubescent, striate or prominantly 10- to 12-ribbed; pappus a single row of white or creamy, stiff, barbellate, capillary bristles (lacking in *P. nanum* and *P. calvum*); chromosome number, $n=30$.

TYPE SPECIES: *Psacalium peltatum* (H.B.K.) Rydb.

This genus is easily recognized by the peltate basal leaves and is the only genus discussed here with stipitate glandular pubescence in addition to the usual nonglandular trichomes.

Key to Species of *Psacalium*

1. Inflorescence and upper portion of stem minutely stipitate glandular; plants also pubescent with nonglandular hairs.
   2. Achenes pubescent.
      3. Corolla tube about twice as long as the lobes, 6–7 mm. long; heads nodding, about 40 or fewer; pappus 9–10 mm. long . . . . **3. P. holwayanum**
      3. Corolla tube about the same length as the lobes, 3.5–4 (–5) mm. long; heads erect, 50 or more; pappus 6–7 mm. long . . . **2. P. eriocarpum**
   2. Achenes glabrous.
      4. Flowers 5–6 per head; phyllaries 5, mostly glabrous or very sparsely pubescent . . . . . **11. P. tabulare**
      4. Flowers 8 or more per head; phyllaries at least as numerous as the flowers, densely pubescent.

5. Basal leaves lobed one-half or less the distance to the center; phyllaries (7–) 8; flowers 8–10; bracts subtending the phyllaries either 3–5 and one-half as long as the phyllaries, or 1 or 2 and as long as the phyllaries.
6. Lobes of the leaves 4 or 5; leaves 5–6 cm. in diameter, pubescent on the adaxial surface; phyllaries subtended by 1 or 2 bracts as long as or longer than thep hyllaries. . . . . **4. P. laxiflorum.**

6. Lobes of the leaves 6 or 7; leaves 20–30 cm. in diameter, glabrous on the adaxial surface; phyllaries subtended by 3–5 bracts about one-half as long as the phyllaries . . . . . **12. P.** species

5. Basal leaves lobed about two-thirds the distance to the center; phyllaries (8–) 12–15; flowers 20 or more; bracts subtending the phyllaries 3 or 4, longer than the phyllaries . . . . . **8. P. peltatum**

1. Inflorescence and upper portion of the stem lacking stipitate glands; plants pubescent with nonglandular trichomes or glabrous.
7. Plants with fleshy underground tubers attached to the caudex.
8. Pappus present, 4–6 mm. long; flowers 5–8; phyllaries 5; plants 0.5 m. tall or taller . . . . . **9. P. peltigerum**

8. Pappus lacking; flowers 10 or 11; phyllaries 7; plants up to about 15 cm. tall . . . . . **6. P. nanum**

7. Plants lacking underground tubers.
9. Pappus lacking; achenes obovoid, 10–12 mm. long, 5–6 mm. wide; leaves deeply and finely dissected almost to the center, the major segments again divided, the ultimate segments linear . **1. P. calvum**

9. Pappus present; achenes ellipsoid, up to 7 mm. long, 2 mm. wide; leaves lobed as deep as three-fourths the distance to the center, not deeply and finely dissected.
10. Phyllaries densely pubescent.
11. Bracts subtending the phyllaries 3 or 4, longer than the phyllaries; phyllaries 8–10; flowers 12 or 13; receptacle naked, not pubescent. **8. P. peltatum**

11. Bracts subtending the phyllaries 3–5, less than half as long as the phyllaries; phyllaries 5; flowers 5 or 6; receptacle sparsely pubescent. **5. P. megaphyllum**

10. Phyllaries glabrous or very sparsely pubescent.
12. Phyllaries 9–10 mm. long; achenes glabrous; leaves pubescent, densely so on the abaxial surface.
13. Phyllaries 5; flowers 5 or 6; ranging from Veracruz west to Michoacán . . . . . **11. P. tabulare**

13. Phyllaries 8 or 9; flowers 10–12; known only from central Oaxaca. **7. P. nelsonii**

12. Phyllaries 5–7 mm. long; achenes pubescent; leaves glabrous or sparsely pubescent along the veins on the abaxial surface. **10. P. poculiferum**

1. Psacalium calvum (Brand.) Pippen, comb. nov.

Cacalia calva Brand. Univ. Calif. Publ. Bot. 4:193. 1911. Holotype: Puebla; Cerro de Gavilan, August 1900, *C. A. Purpus* 4113 (UC, not seen; isotypes GH!, US!).

Odontotrichum calvum (Brand.) Rydb. Bull. Torrey Bot. Club 51:420. 1924.

Lower portion of the plant not seen; plants ca. 0.5 m. tall; stem and leaves densely pubescent to tomentose; flowering stem terete;

basal (?) leaves 2 or 3, long-petioled, peltate, subcircular in outline, 12–14 cm. in diameter; blades deeply dissected into 6–8 divisions extending almost to the center, the major divisions several times subdivided, the ultimate divisions narrow, linear; petioles slender, 20–25 cm. long; cauline leaves reduced and bracteiform; inflorescence corymbose, the branches subtended by linear-subulate bracts to 1 cm. long; heads about 20; phyllaries 12, narrowly ovate, 8 mm. long, 1 mm. wide; flowers 12–14; corolla about 7–8 mm. long (flower measurements from the original description), the tube 3–4 mm. long, the throat ca. 0.5 mm. long, 0.5–1 mm. across at the apex, the lobes 4 mm. long; anthers about 3 mm. long; style branches recurved, hirtellous; mature achenes obvoid, 10–12 mm. long, 5–6 mm. wide, glabrous, pale brown; pappus lacking entirely.

DISTRIBUTION: Known only from the type specimens.

The specimens examined lacked adequate flowering material, and the poorly preserved leaves made it difficult to determine whether or not they were peltate.

The most unusual features of this species are the extremely large, obovoid achenes and lack of a pappus. Field examinations and study of material collected in the future may indicate a change in the taxonomic position of this taxon.

2. Psacalium eriocarpum (S. F. Blake) Blake Journ. Wash. Acad. Sci. 28:492. 1938.
Cacalia eriocarpa S. F. Blake Journ. Wash. Acad. Sci. 129. 1929. Holotype: Jalisco; Arroyo de Santa Gertrudis, San Sebastian, steep slopes in open pine and oak woods, 1,500 m., Jan. 21, 1927, *Ynez Mexia* 1539 (US!).

Slender plants up to 1.3 m. tall, stems 5–10 mm. thick at the base, purplish green, sparsely or densely pubescent with long, multicellular, stiff, attenuate-tipped hairs, 1–1.5 mm. long, and with multicellular, stipitate glands, 0.5 mm. long; leaves hirsute with nonglandular hairs like those on the stem, the pubescence denser on the adaxial surface; basal leaves 2 or 3, long-petioled, centrally peltate, subcircular in outline, 15–25 (–30) cm. in diameter, the venation radiate with 10 or 11 principal veins; blades shallowly lobed one-third the distance to the center of the blade or less, the lobes 8–10, 1.5–2 times broader than long, each 3-angulate or subdivided into 2 or 3 smaller lobules, the margins spinulose-toothed or entire, the center of the blade flat, not depressed; petioles 15–30 cm. long, slender; cauline leaves 1 or 2, greatly reduced, bracteiform, inflorescence paniculate, usually 30 cm. long or longer, 10–15 cm. broad, the branches subtended by narrowly triangular bracts 3–7 mm. long, 1 mm. wide; pedicels 3.5–5 (–9) mm. long, calyculate bracts 3–5, subulate, 2–5 mm. long; heads 50–70 (–90), 1.2–1.5 cm. long; phyllaries 5 or 8, narrowly ovate or elliptic, (6–) 7–8 (–9) mm. long, 1–3 mm. wide, purplish tipped, pubescent, occasionally sparsely stipitate glandular; flowers 6 (when 5 phyllaries)

or 9–11 (when 8 phyllaries); corolla about 8–9 mm. long, the tube (3.5–) 4 (–5) mm. long, the throat short, campanulate, about 1 mm. long and broad, the lobes about as long as the tube, 3–4 (–5) mm., narrowly triangular; anthers 3–4 mm. long; style branches 1.5–2 mm. long, the abaxial surface hispidulous, especially distally, the tips rounded or obtuse with a sparse subterminal fringe of hairs; mature achenes not seen, the immature achenes pale green, densely villous; pappus (5.5–) 6–7 (–8) mm. long, white; chromosome number, $n=30$ (Pippen).

DISTRIBUTION: Western Jalisco. Mostly in pine and, less frequently, oak woodlands. Flowering mid-November to December.

This species has two forms: the more common form has small heads with 5 phyllaries and 6 flowers, the other has larger heads with 8 phyllaries and 9–11 flowers. These two forms are similar in all other aspects, including range. The larger headed form is known only from an area in between the known populations of the smaller headed form. These forms are not given nomenclatural status. This species is closely related to *P. holwayanum* but differs from it in the smaller heads, erect inflorescence, and less deeply lobed leaves.

JALISCO: *McVaugh* 13954, 14287, 13684, 14165 (MICH); *McVaugh & Koelz* 919 (MICH); *Pippen* 36, 62*, 66, 67 (MICH).

3. Psacalium holwayanum (B. L. Rob.) Rydb. Bull. Torrey Bot. Club 51:372. 1924.

Cacalia holwayana B. L. Rob. Proc. Amer. Acad. 43:45. 1907. Holotype: Michoacán; Uruapan, Oct. 11, 1899, *E. W. D. Holway* 2617 (GH!).

Psacalium langlassei Rydb. Bull. Torrey Bot. Club: 51:376. 1924. Holotype: Guerrero; Sierra Madre, in 1898, *E. Langlassé* 576 (US!).

Plants up to 1 m. tall; stems 3–5 mm. thick at the base, densely pubescent with stiff, white hairs up to 2 mm. long, 12- to 20-celled, and also with 6-celled stipitate glands, 0.1–0.2 mm. long, abundant distally; leaves sparsely or densely pubescent with stiff, nonglandular hairs only; basal leaves 2 or 3, long-petioled, peltate, subcircular in outline, (9–) 12–14 (–26) cm. in diameter, the venation radiate with 8 principal veins; blades lobed about one-third the distance to the center, the lobes 7 or 8, 2.5–4 cm. long, 3–6 cm. wide, each one 3-angulate or divided into 2 or 3 smaller secondary lobes, the margins irregularly and sparsely toothed; petioles (9–) 10–18 (–32) cm. long, terete; cauline leaves 2 or 3, similar to the basal ones but smaller, 1–5 cm. in diameter, the uppermost subpeltate with petioles 1–5 (–10) cm. long; inflorescence thyrsiform, 16–30 cm. long, 14–16 cm. broad, the branches pubescent and stipitate glandular like the stem, subtended by either linear bracts 1–2 cm. long, 1 mm. wide or occasionally spathulate bracts, 3-toothed at the tip; pedicels 5–15 mm. long;

calyculate bracts 3–5, subulate, 4–7 mm. long; heads about 40 or fewer, nodding, 1.5–3 cm. long; phyllaries 8, narrowly ovate, 9–13 mm. long, 1.5–3 mm. wide, purplish, pubescent with glands and sparsely hirsute with nonglandular, long, stiff hairs; receptacle 3–3.5 mm. long; flowers 10 or 11; corolla 10–11 mm. long, the tube 6–7 mm. long, the throat short, campanulate, ca. 1 mm. long, 1.5–2 mm. across, the lobes 3–3.5 (–5, *Pringle* 13294) mm. long, linear, 0.5 mm. wide, anthers 3.5–4 mm. long; style branches 1.5–2 (–3) mm. long, hispid on the abaxial surface, the tips truncate with a terminal fringe of trichomes; mature achenes 5–6 mm. long, 1.5 mm. wide, 0.5–0.7 mm. thick, oblong, or ellipsoid, pale, densely pubescent with unicellular, adpressed, ascending hairs; pappus 9–10 mm. long, white; chromosome number, $n=30$ (Turner, ined.).

DISTRIBUTION: Known from west central Michoacán eastward to México and from one collection in Guerrero. Mostly in pine woodlands. Flowering mid-November to December.

An isoparatype, *Langlassé* 576 (US), was described by Rydberg as *Psacalium langlassei*, because the leaves were less deeply lobed. Comparison of this specimen with the type and other specimens of *P. holwayanum* indicates that they are conspecific because they are similar in all characters except leaf lobes. The specimen Rydberg examined was merely less deeply lobed.

GUERRERO: *Langlassé* 576 (GH, paratype of *C. holwayana*, isotype of *P. langlassei*). MÉXICO: *Gilly* 5 (MICH); *Matuda* 30015 (NY). MICHOACÁN: *King & Soderstrom* 4890 (MICH); *Pringle* 13297 (GH, US), 13672 (GH, paratype; US), 13979 (GH, MICH, US); *McVaugh* 21953* (MICH).

4. Pascalium laxiflorum Benth. Pl. Hartw. 41. 1841. Holotype: Michoacán; Morelia, pine woods, in 1836, *Hartweg* 318 (K, not seen; Field Mus. Neg. 37949!).

Senecio moreliae Hemsl. Biol. Centr. Amer. Bot. 2:243. 1881. Based on *Psacalium laxiflorum* Benth. not *S. laxiflorum* Viv.

Slender plants 6–7 cm. tall; stems 3–4 mm. thick at the base, pubescent with multicellular stiff hairs, 1–1.5 mm. long, and minute, 2- to 3-celled stipitate glands ca. 0.1 mm. long, most abundant distally; leaves pubescent on the adaxial surface with nonglandular hairs, subglabrous abaxially; basal leaves 2 or 3, petiolate, peltate, subcircular in outline, 5–6 cm. in diameter, the venation radiate with 5 principal veins; blades lobed about one-half the distance to the center, the lobes 4 or 5, 1–2 cm. long and broad or occasionally 1.5–2 times broader than long, each slightly 3-angulate, the tips rounded or obtuse, the margins mucronulate-toothed, the sinuses broadly rounded; petioles 6–8 cm. long, terete; cauline leaves usually 2, the lowermost similar to the basal ones, the upper one nonpeltate, 2.5–4 cm. long, 1–2 cm. wide with the petiolar portion leafy-margined,

ovate, the blade portion 3-lobed; inflorescence paniculate, 16–26 cm. long, 11–12 cm. broad, the branches pubescent and stipitate glandular like the stem, subtended by narrowly ovate or ovate bracts 2–2.5 cm. long, 0.5–1 cm. wide progressively smaller upward, the bracts glandular on the adaxial surface, glabrous abaxially; pedicels 5–10 mm. long; calyculate bracts 1–2, subulate, 8–10 mm. long; heads 30 or fewer, 14–15 mm. long; phyllaries 8, narrowly ovate, (6–) 7–8 mm. long, 1.5–3 mm. wide, purplish, densely stipitate glandular; flowers 8; corolla 8–9 mm. long, the tube 5–5.5 mm. long, the throat ampliate, 0.5 mm. long, 0.7–1 mm. wide, the lobes 3–3.5 mm. long, linear; anthers 3 mm. long; style branches 1.5 mm. long, hispid on the abaxial surface, the tips truncate or rounded with a terminal or subterminal fringe of trichomes; mature achenes not seen, immature achenes glabrous, striate; pappus 6–7 mm. long, white.

DISTRIBUTION: Known only from the type collection and one collection from southern Durango (*Rose* 2337, GH, US). In pine-woodlands. Flowering in August.

This species has smaller leaves than the other members in the section, and they tend to be 4-lobed and somewhat cross shaped. It is related to *P. holwayanum* and *P. eriocarpum*.

5. Psacalium megaphyllum (Rob. & Greenm.) Rydb. Bull. Torrey Bot. Club 51: 374. 1924. PLATE 6

Cacalia megaphylla Rob. & Greenm. Amer. Journ. Sci. III. 50:157. 1895. Holotype: Jalisco; on hillside near Guadalajara, Oct. 10, 1889, *C. G. Pringle* 2490 (GH!).

Cacalia obtusiloba Rob. & Greenm. Amer. Journ. Sci. III. 50:158. 1895. Holotype: Oaxaca; Sierra de San Felipe, 6,000 ft., Nov. 17, 1894, *C. G. Pringle* 5840 (GH!).

Psacalium obtusilobum (Rob. & Greenm.) Rydb. Bull. Torrey Bot. Club 51:374. 1924.

Stout plants to 3 m. tall; entire plant pubescent, the pubescence denser in the inflorescence and on the abaxial surface of the leaves, the hairs 0.5–0.7 mm. long, 5- to 15-celled, white; stem to 2 cm. thick at the base; basal leaves 3 or 4, long-petioled, peltate, subcircular in outline, 30–60 cm. in diameter, the venation radiate with 5–7 principal veins; blades lobed one-half to two-thirds the distance to the center, the primary lobes 5–7, 7–15 cm. long from the base of the sinus to the distal edge, 5–7 cm. wide at the base, each usually divided into 3 lobes, the secondary lobes (5–) 7–10 cm. long, 3–5 cm. wide at the base, each divided into several smaller, triangular lobules 1–3 cm. long, the margins coarsely toothed, the center of the blade depressed; petioles 25–80 cm. long, terete, purplish green; cauline leaves 5–7 or more, the lowermost usually smaller than the basal ones but similar to them, 30–35 cm. in diameter, the upper cauline leaves progressively smaller upward, subpeltate or nonpeltate, the

uppermost 8–15 cm. long, 10–20 cm. wide, palmately 3- to 5-lobed, the petioles 3–7 cm. long; inflorescence broadly paniculate-corymbose, to 1.5 m. high, ca. 1 m. broad, the proximal branches in the axils of the uppermost leaves, the distal branches subtended by ovate bracts 2–5 cm. long, 3–7 mm. wide; pedicels about as long as the phyllaries; calyculate bracts 3–5, subulate, 1.5–2 mm. long; heads at least 150, 10–12 mm. long; phyllaries 5, narrowly elliptic or narrowly ovate, (5.5–) 7–8 (–10) mm. long, (1.5–) 2–3 mm. wide, densely white puberulent; receptacle sparsely pubescent with filiform, multicellular hairs; flowers 5 (–6); corolla 6–8 mm. long, the tube 3–4 mm. long, the throat 0.5 mm. long and broad (or occasionally lacking), the lobes narrowly triangular, 2.5–4 (–5.5) mm. long, reflexed; anthers 2–3.5 mm. long; style branches 1–1.5 mm. long, the abaxial surface hispid, denser distally, the tips obtuse with a sparse terminal fringe of trichomes; mature achenes oblong or ellipsoid, 5–5.5 mm. long, 1.5–2 mm. wide, 1 mm. thick, pale green, glabrous, 15- to 20-ribbed; pappus 4–5 (–7) mm. long, white; chromosome number, $n=30$ (Turner, ined.).

DISTRIBUTION: From Zacatecas southeast to Oaxaca. Common, at least in western Mexico, in rocky grasslands, roadsides, and grazed areas. Flowering in September and October.

This species is striking because of its very large size and especially its extremely large basal leaves, depressed in the center. Most existing herbarium specimens do not adequately represent the species because even one leaf is larger than the average herbarium sheet.

Robinson and Greenman in describing *Cacalia megaphylla* and *C. obtusiloba* stated that the latter differed from the former in having smaller heads and more rounded basal leaf lobes. Comparison of the types of these two species, however, indicates that they are conspecific because of several common characters: Number of phyllaries and flowers, pubescence of phyllaries, leaves and stem, general habit, and leaf shape (the latter somewhat variable).

AGUASCALIENTES: *McVaugh & Koelz* 39 (MICH); *Pippen* 8* (MICH). GUERRERO: *McVaugh* 21897, 21910 (MICH); *Moore* 5119 (MICH). JALISCO: *McVaugh* 13321 (MICH); *Pippen* 16, 24, 39 (MICH). MÉXICO: *Hinton* 2200 (US), 2355 (NY); *Matuda* 26572 (NY). MICHOACÁN: *Arsène* 2386 (US); *Hinton et al.* 13480, 15629 (MICH, NY); *Pippen* 47 (MICH); *McVaugh* 21928 (MICH). MORELOS: *Pringle* 6165 (GH, NY, US). NAYARIT: *Mexia* 877 (GH, MICH, US). PUEBLA: *Arsène & Nicholás* 334 (US); *Arsène,* s.n., November 1908 (US). ZACATECAS: *McVaugh* 17650 (MICH).

6. Psacalium nanum Pippen, sp. nov. PLATES 7, 8

Plantae nanae usque ad 12 cm. altae, tuberibus pluribus, carnosis, fusiformibus, subterraneis, caulibus hirsutis scaposis, foliis radicalibus peltatis, suborbicularibus, usque ad 5 cm. diametro, profunde 7-

lobatis, supra hirsutis, subtus glabris, petiolis tenuibus 5–10 cm. longis hirsutis; inflorescentia corymbosa, 2–3 cm. longa latasque, bracteis foliosis, trullatus, usque ad 2 cm. longis; capitula usque ad 25, ca. 7 mm. longa; phyllaria 8, elliptica 3.5–4.5 mm. longa, glabra; flores 10–11, corollis 3.5–4 mm. longis, tubo 1.5–2 mm. longo, lobis 2–3 mm. longis; achaenia matura non visi; pappus nullus.

Plants scapose, up to 12 cm. tall with several fleshy, elongate, fusiform tubers attached to the caudex beneath the soil; stems, petioles, and adaxial surface of the leaves hirsute with tawny multicellular hairs to 1.5 mm. long, the abaxial surface of the leaves glabrous; stems slender, 2 mm. thick at the base; basal leaves 7–15, long-petioled, centrally or subcentrally peltate, subcircular in outline, to 5 cm. across, the venation radiate with 7 principal veins; blades deeply lobed one-half to two-thirds the distance to the center of the blade, the primary lobes 7, each divided into 3 major lobes and 2 or 3 lesser lobules, the secondary lobes often again lobed, the ultimate segments triangular, mucronate; petioles slender, 5–10 cm. long; inflorescence corymbose, 2–3 cm. long and broad, tightly compact, the primary branches subtended by petiolate, leafy bracts up to 2 cm. long, the blade portion obtrullate; pedicels mostly glabrous; calyculate bracts usually 3, subulate, up to 1.5 mm. long; heads 25 or fewer, about 7 mm. long; phyllaries 7, elliptic, 3.5–4.5 mm. long, 0.7–1 mm. wide, glabrous; flowers 10 or 11; corolla, 0.7–1 mm. wide, elliptic, strongly 3-nerved, the throat none; anthers 2 mm. long; style branches 0.7 mm. long, hispid on the abaxial surface, the tips truncate or rounded with a terminal or subterminal fringe of trichomes; mature achenes not seen, the immature achenes brown, glabrous, 10-ribbed; pappus entirely lacking.

HOLOTYPE: Guerrero; Teitepec (Mina Distr.). Open stunted pine forest, on mossy rocks, 3,600 m. (acc. to the label), July 17, 1939, *G. B. Hinton et al.* 14464 (US!, isotypes MICH!, NY!).

DISTRIBUTION: Known only from the type collection. Flowering in July.

This species has affinities with both *P. peltigerum* (through the underground tubers) and *P. calvum* (through the lack of a pappus). The small size makes this species unique in this genus.

7. **Psacalium nelsonii** Rydb. Bull. Torrey Bot. Club 51:374. 1924. Holotype: Oaxaca; vicinity of Cerro de San Felipe, 9,500–11,000 ft., in 1894, *E. W. Nelson* 1111 (US!).

Roots, base of plant and stem below the inflorescence not seen; leaves, presumably basal, petioled, peltate, subcircular in outline, 30–35 cm. in diameter, the venation radiate with 7 or 8 principal veins; blades lobed about one-half the distance to the center of the blade, slightly longer than wide, each divided into 2 or 3 secondary lobes

which are obtusely deltoid, mucronate-tipped, the adaxial surface pubescent with multicellular hairs up to 1.5 mm. long, the abaxial surface gray-tomentose; cauline leaf (only one seen) similar to the basal leaves but subpeltate, the petiole attached 2–3 mm. above the base of the blade, the blade 8-lobed; inflorescence paniculate, at least 35 cm. long, 15 cm. broad, the branches purple-tomentose, the tomentum denser toward the heads, the branches subtended by leafy bracts, 4–10 cm. long, obovate, palmately 3- to 7-lobed or subentire; calyculate bracts about 5, linear-subulate, 4–5 mm. long; heads many, about 12 mm. long; phyllaries 8 or 9, elliptic, narrowly ovate or oblong, 10 mm. long, 2–3 mm. wide, glabrous, purplish tinted; flowers mostly immature, 10–12; corolla about 7 mm. long, purplish tinted when dry, the tube 3.5–4 mm. long, the throat 0.5–1 mm. long, 1–1.5 mm. broad, the lobes 3 mm. long; anthers 2–3 mm. long; style branches 1.5 mm. long; mature achenes not seen, the immature achenes glabrous; pappus white, about 5 mm. long.

DISTRIBUTION: Known only from the type specimen. Flowering time unknown.

The type collection consists only of a basal leaf and a portion of the inflorescence. It is apparently related to *P. peltatum* because of the leafy inflorescence bracts, the number of phyllaries and flowers, and the glabrous achenes. It differs from *P. peltatum* because of the glabrous phyllaries, short subinvolucral bracts, tomentose condition of the leaves, and the outline of the basal leaves. This specimen appears to be significantly different from any of the known species of *Psacalium* and therefore I have followed Rydberg in recognizing it as a distinct species, despite the incomplete condition of the type specimen.

8. **Psacalium peltatum** (H.B.K.) Cass. Dict. Sci. Nat. 43:461. 1826.
   Cacalia peltata H.B.K. Nov. Gen. et Sp. 4:170. t. 361. 1820. (Folio ed. 4:133. 1820.)
   Senecio peltiferus Hemsl. Biol. Centr. Amer. Bot. 2:245. 1881. Based on *Cacalia peltata* H.B.K., not *S. peltatus* DC.

Plants up to 2.5 m. tall; stems and leaves sparsely to densely pilose or hirsute with multicellular, conical-attenuate nonglandular hairs, 0.5–2 mm. long, the crosswalls often purple, the stems also occasionally densely covered with minute, multicellular stipitate glands, 0.3–0.5 mm. long, (lacking in var. *peltatum*); stems stout, terete; basal leaves 3 or 4, long-petioled, peltate, subcircular in outline, 10–30 (–65) cm. in diameter, the venation radiate with 6–8 principal veins; blades deeply lobed about two-thirds the distance to the center, the primary lobes 7–9, each sinuately 5- to 7-lobed, the distal secondary lobes often larger than the others, again lobed or 3-angulate; lowermost cauline leaves similar to the basal ones and about as large; upper cauline

leaves progressively smaller upward, subpeltate, the uppermost non-peltate with leafy-margined petioles, the blade palmately 3- to 5-lobed; inflorescence racemose, paniculate or corymbose, the branches densely stipitate-glandular, subtended by sessile, leafy bracts, ovate or narrowly ovate, less often linear; heads 10–100, 1.5–2.5 cm. long, phyllaries 8–10 or 12–14, pubescent; the involucre subtended by 3 or 4 narrowly ovate or linear bracts longer than the phyllaries; flowers 12–20 (–40); corolla about 9–14 mm. long, the tube 6–10 mm. long, the throat ampliate, 0.5 mm. long, 1–1.5 mm. broad, the lobes narrowly triangular, 3–4 mm. long; anthers 3–3.5 (–4) mm. long; style branches 1.5–2 mm. long, recurved, hispid on the abaxial surface, the tips truncate or obtuse with a sparse subterminal fringe of trichomes; mature achenes oblong or ellipsoid, 5.5–7 mm. long, 1–1.5 mm. wide, 0.7–1 mm. thick, glabrous, creamy, multistriate; pappus 6–8 (–9) mm. long, white.

This is a variable and complex species usually distinguished by the sessile, elliptic or lobed inflorescence bracts, the 3 or 4 long, calyculate bracts subtending the phyllaries, the creamy, glabrous achenes, and the usually deeply lobed basal leaves.

Within this complex are three smaller groups, recognized as varieties, which seem to maintain themselves both morphologically and geographically.

Of several other specimens that are apparently a part of this complex, two are quite similar to var. *conzattii* and are discussed with that taxon. Another specimen is unique (Guerrero, between Petlacala and Buenavista, *G. B. Hinton* 14877, MICH, NY) and is from a poorly explored region where no specimens of *P. peltatum* have been collected. This specimen has much less deeply lobed leaves with much broader lobes than *P. peltatum* but with an inflorescence like var. *peltatum*, except it is glandular-pubescent. More material from this region as well as field observations will be necessary to determine the best taxonomic position of this plant.

Key to Varieties of *Psacalium peltatum*

1. Stem and inflorescence glandular pubescent, the glands stipitate, 0.5 mm. long; plants also pubescent with long, stiff, nonglandular hairs.
   2. Heads few, ca. 10, 2–2.5 cm. long; calyculate bracts 15–17 (–25) mm. long; pappus bristles 7–9 mm. long; flowering in September and October.
      8c. P. peltatum var. conzattii
   2. Heads many, at least 50, ca. 1.5 cm. long; calyculate bracts 20–35 mm. long, pappus bristles 6–7 mm. long, flowering in July and August.
      8b. P. peltatum var. adenophorum
1. Stem and inflorescence lacking stipitate glands but sparsely to densely hirsute or pilose with nonglandular hairs . . . **8a. P. peltatum var. peltatum**

8a. Psacalium peltatum var. **peltatum**

Cacalia peltata H.B.K. as to holotype: Michoácan; in woods around Pázcuaro [Pátzcuaro], 1130 hex., *Humboldt & Bonpland* 4346 (P, not seen; Field Mus. Neg. 37873!).

Cacalia peltata var. *coulteri* Greenm. Proc. Amer. Acad. 40:51. 1904. Lectotype: Hidalgo (Veracruz on the label); Real del Monte, *Th. Coulter* 420 (GH!).

Psacalium coulteri (Greenm.) Rydb. Bull. Torrey Bot. Club 51:373. 1924.

Psacalium argutum Rydb. Bull. Torrey Bot. Club 51:373. 1924. Holotype: San Luis Potosí, in 1879, *J. G. Schaffner* 725 (NY!).

Stems and leaves sparsely or densely pilose or hirsute with non-glandular, multicellular trichomes, 0.5–2 mm. long, the stem and inflorescence not stipitate glandular; basal leaf lobes (7–) 10–12 (–20) cm. long, 3–5 cm. wide at the base, the sinuses obtuse or broadly rounded; petioles (10–) 20–40 cm. long, the petiole of the lowermost cauline leaf more dilated than those of the basal leaves, and leafy-margined; inflorescence paniculate or corymbose, about 1 m. long and broad, the leafy bracts ovate, 3–4 (–7) cm. long, 2–3 cm. broad, occasionally 3-lobed near the distal end; calyculate bracts narrowly ovate or ovate, (11–) 12–17 (–25) mm. long, one of these usually broader than the others surrounding the same head; heads many, ca. 15 mm. long; phyllaries 8–10, narrowly ovate, 10–12 (–15) mm. long, 2–3 mm. wide, pubescent but not stipitate glandular; flowers 12–17 (–20); corolla 8.5–10.5 mm. long, the tube (5.5–) 6–7 mm. long, the lobes 3–3.5 mm. long, 1 mm. wide; anthers 3.3–5 mm. long, pappus 7–8 mm. long; chromosome number, $n=30$ (Pippen).

Distribution: From southern Chihuahua south through Durango to Jalisco, eastward across the Trans-Mexican volcanic belt in Michoacán and México to Puebla. Grassland openings and borders of the pine woodlands. Flowering September and October.

The pubescence varies from sparsely short puberulent to densely pilose or villous. Greenman distinguished the villous specimens as var. *coulteri*. Apparently this was the only character used and it does not appear to be consistent or correlated with any other characters, therefore, I have not recognized the var. *coulteri*.

Rydberg distinguished *Psacalium argutum*, a group of specimens from San Luis Potosí, as differing from *P. peltatum* by the presence of longer calyculate bracts and more sharply pointed basal leaf lobes. Although such a tendency is noted in these specimens, it is neither consistent nor restricted to this region. There are no other significant differences in these specimens and I have not supported this separation.

Chihuahua: *Gentry, Correll, & Arguelles* 18016 (US). Durango: *Nelson* 4954 (NY, US); *Pennell* 18343 (NY); *Iberra Garcia* 414 (US). Distrito Federal: *Matuda* 26175, 26632 (NY). Hidalgo: *Pringle* 9870 (GH). Jalisco: *McVaugh* 13821 (MICH). México: *Hinton* 1908 (US); *Matuda* 28343, 29483, 29591 (NY); *Rose & Painter* 7939 (GH, US, paratypes of v. *coulteri* Greenm.); *Lyonnet* 3122

(US). MICHOACÁN: *Nelson* 6582 (GH, NY, US); *Pippen* 44, 49*, 53 (MICH); *Pringle* 3340 (GH, NY, US); *Seler* 1259 (GH, NY, US). MORELOS: *Lyonnet* 794 (US); *Pringle* 9871 (GH, MICH, NY, US). PUEBLA: *Beaman* 3619 (TEX); *Purpus* 3038 (NY, US). SAN LUIS POTOSÍ: *Schaffner* 294 (GH); *Parry & Palmer* 543 (GH, NY, US). TLAXCALA: *Sharp & Hernández X.* 44508 (NY). VERACRUZ: *Seaton* s.n., August 1891 (GH, paratype of v. *coulteri* Greenm.).

8b. Psacalium peltatum var. adenophorum S. F. Blake, Journ. Wash. Acad. Sci. 32:150. 1942. Holotype: Nuevo Leon: Municipio de Rayones, upper west slopes of Sierra de Cebolla, above 2,750 m., Aug. 21, 1939, *C. H. Muller* 2911 (US!).

Plants ca. 1.5 m. tall; stems and leaves sparsely or densely pilose or hirsute with multicellular, nonglandular hairs, the stem and inflorescense also densely covered with minute stipitate glands; stem 5–9 mm. thick at the base; leaves similar to those of the typical variety; inflorescence paniculate or corymbose, ca. 30 cm. long, 11–17 cm. broad, the bracts up to 6 cm. long, 1.5 cm. broad; calyculate bracts 2.0–3.5 cm. long, 3–10 mm. wide; heads ca. 40, about 2 cm. long; phyllaries (8–) 12 or 13, narrowly ovate, (10–) 15–16 mm. long, 2–3 mm. wide; flowers ca. 20; corolla 13–14 mm. long, the tube (7–) 9–10 mm. long, the lobes ca. 4 mm. long; anthers 3–3.5 mm. long; mature achenes not seen; pappus 6–7 mm. long.

DISTRIBUTION: Known only from the southern region of Nuevo Leon and Tamaulipas. Flowering in July and August.

This taxon is known from only one collection in addition to the type (Tamaulipas: *Stanford, Taylor, & Lauber* 2535, NY, TEX, US). The longer subinvolucral bracts and presence of stipitate glands separate it most easily from the typical variety. Time of flowering and geographical range separate it from var. *conzattii*.

8c. Psacalium peltatum var. **conzattii** (Rob. & Greenm.) Pippen, comb. nov.

Cacalia peltata var. *conzattii* Rob. & Greenm. Proc. Amer. Acad. 32:49. 1896. Lectotype: Oaxaca; Sierra de San Felipe, 10,000 ft., Dec. 13, 1895, *C. G. Pringle* 6238 (GH!).

Psacalium conzattii Rydb. Bull. Torrey Bot. Club 51:372. 1924.

?*Psacalium mollifolium* S. F. Blake, Journ. Wash. Acad. Sci. 28:491. 1938. Holotype: Guerrero; Taxco, Aug. 12, 1937, *Ruth Q. Abbott* 353 (GH!).

Plants usually 1 m. tall or less; stems and leaves sparsely or densely pilose or hirsute with nonglandular trichomes, these especially dense on the abaxial surface of the leaves, the stem and inflorescence also densely stipitate-glandular; stem 4–10 mm. thick at the base; basal leaves subcircular, 14–25 cm. in diameter; blades deeply lobed usually more than three-fourths the distance to the center, the primary lobes 4–10 cm. long, 2–4 cm. wide at the base; inflorescence subpaniculate 10–20 (–30) cm. long, 11–16 cm. broad, the branches subtended by bracts about 3 cm. long, 0.7–1.5 cm. wide; calyculate bracts narrowly elliptic, 15–17 (–25) mm. long, 1–2.5 mm. wide; heads usually 10

(–30), 2–2.5 cm. long; phyllaries 12–15, narrowly ovate, 12–15 (–18) mm. long, 2–3 (–4) mm. wide, pilose with nonglandular hairs, stipitate-glandular; flowers (20–) 25–40; corolla 10–12 mm. long, the tube (6–) 7–8 (–9) mm. long, the lobes 3.5–4 mm. long, 1 mm. wide; anthers 3–3.5 (–4) mm. long; mature achenes 6–7 mm. long, 1–1.5 mm. wide, ca. 10-ribbed; pappus 7–8 (–9) mm. long.

DISTRIBUTION: Known mostly from central Oaxaca and questionably from Guerrero and Durango. Openings in pine woodlands. Flowering in September and October.

Two specimens were cited in the original description as syntypes: Oaxaca; Cerro de San Felipe, 9,000 ft., Nov. 29, 1895, *C. Conzatti* 27 (GH!), Dec. 13, 1895, *C. G. Pringle* 6238 (GH!). Despite the fact the taxon was named for Conzatti, possibly indicating his specimen as the lectotype, *Pringle* 6238 is a more complete and more representative specimen and is thus a better choice for the lectotype.

Two specimens have been studied that are obviously closely related to this taxon but differ in certain respects. One specimen (15 mi. W. of El Salto, *U. T. Waterfall* 12688, MICH) has heads and stipitate glands like var. *conzattii* but the leaves are smaller with obovate lobes; most significant is its occurrence in Durango which is quite far from Oaxaca. Such a separation in range is difficult to explain if this specimen is a part of this taxon.

The other specimen (Guerrero: Taxco, *Ruth Q. Abbott* 353, GH) was the basis of *Psacalium mollifolium* S. F. Blake. It differs from var. *conzattii* in that the basal leaves are lobed less than half the distance to the center and the abaxial surface is densely tomentose. The inflorescence is similar to var. *conzattii*, including the long calyculate bracts. These differences do not appear significant enough to give this specimen nomenclatural status; at least not until field observations and study of future material can be made.

OAXACA: *Pringle* 6238 (US, isotype); *Camp* 2401 (NY); *McVaugh* 21826 (MICH).

9. Psacalium peltigerum (Rob. & Seat.) Rydb. Bull. Torrey Bot. Club 51:374. 1924.

Cacalia peltigera Rob. & Seat. Proc. Amer. Acad. 28:111. May 13, 1893.

Plants up to 1.5 m. tall with several fleshy underground tubers up to 5 cm. long, 3 cm. thick attached to the caudex; stems 5–12 mm. thick at the base, mostly glabrous or sparsely hirsute; leaves sparsely or densely pubescent with stiff, white hairs up to 1 mm. long; basal leaves 2 or 3, long-petioled, peltate, subcircular in outline, (10–) 20–30 cm. in diameter, the venation radiate with 7–9 (–12) principal veins; blades angulate or lobed one-third to four-fifths the distance to the center, the primary lobes 9–11, each divided into 2 or 3 major lobes and several lesser lobules, the secondary lobes usually lobed or coarsely

toothed, or if the blade angulate the margins mucronate-tipped; petioles 29–30 cm. long, pubescent proximally, becoming glabrous toward the blade; cauline leaves 3 or 4, the lowermost similar to the basal ones but smaller; upper cauline leaves progressively smaller upward, either nonpeltate with the blades 3- to 7-palmately lobed or remaining peltate and angulate, not lobed; inflorescence mostly corymbose, 9–30 cm. long and broad, the branches subtended by linear-subulate bracts, 1.5–2 cm. long, 1–2 mm. wide; pedicels 1–2 cm. long; calyculate bracts 3–5, subulate, 2 (–5) mm. long; heads many, 12–15 mm. long; phyllaries 5, narrowly oblong, narrowly elliptic, or occasionally spathulate, (6–) 7–8 (–10) mm. long, 1–2 mm. wide, glabrous; receptacle 1–1.5 mm. across; flowers 5 or 6; corolla 9–10 mm. long, the tube (3.5–) 4–5 mm. long, the lobes as long as the tube or slightly longer, narrowly elliptic, the throat none; anthers 3–3.5 mm. long, style branches 1–1.5 mm. long, distally hispid on the abaxial surface, the tips truncate or rounded with a subterminal or terminal fringe of trichomes; mature achenes ellipsoid, 4–5.5 mm. long, 1.5–2 mm. thick, glabrous, tan, prominently 10-ribbed; pappus (4–) 5–5.5 (–6) mm. long, creamy or tawny.

This species is easily distinguished by the presence of fleshy subterranean tubers. Microscopic examination of freehand sections reveals that these tubers are modified stems with discrete vascular bundles. Druse-shaped crystals were found in the parenchyma cells. In greenhouse-grown plants these tubers formed during the first season of growth and persisted through the dormant period. There is no evidence that they function in vegetative propagation as do the tubercles in the genus *Pericalia*.

Three varieties are recognized and may be separated primarily by the outline of the basal leaves and geographical distribution. These three varieties exhibit an interesting range in leaf shapes from almost entire (var. *hintonii*), to broadly lobed (var. *laxilobum*), to deeply linear-lobed, the lobes five times longer than broad (var. *peltigerum*).

Key to Varieties of *Psacalium peltigerum*

1. Basal leaves angulate, not lobed, the margin with mucronate tips; stem hirsute . . . . . **9b. P. peltigerum var. hintonii**

1. Basal leaves lobed at least half the distance to the center, the margins toothed, the teeth triangular, not mucronate; stems mostly glabrous or very sparsely hirsute.
   2. Lobes of the basal leaves extending two-thirds to four-fifths the distance to the center of the blade, 1–2 cm. wide at the base, much longer than broad, the ultimate segments of the lobes narrowly triangular or linear-attenuate, about 5 times longer than wide; stem glabrous.
      9a. P. peltigerum var. peltigerum

2. Lobes of the basal leaves extending less than one-half the distance to the center of the blade, 5–7 cm. wide at the base, about as long as wide, the ultimate segments of the lobes obtusely deltoid or triangular, about as long as broad; stem hirsute at least on the proximal half.
9c. P. peltigerum var. **latilobum**

9a. Psacalium peltigerum var. **peltigerum**

Cacalia peltigera Rob. & Seat. as to Holotype: Jalisco; bluff of the barranca near Guadalajara, Sept. 14, 1891, *C. G. Pringle* 5154 (GH!).

Blades of the leaves deeply lobed two-thirds to four-fifths the distance to the center, the primary lobes 9–11, 1–2 cm. wide at the base, much longer than wide, each subdivided into 2 or 3 major lobes and several lesser lobules, the secondary lobes usually lobed or coarsely toothed, the ultimate segments narrowly triangular or linear-attenuate, ca. 5 times longer than wide.

DISTRIBUTION: Central and western Jalisco. In the dry grasslands around Guadalajara and the pine woodlands to the west. Flowering in July and August.

In the original description two specimens were listed as syntypes: Jalisco; Río Blanco, July 1886, *E. Palmer* 171 (GH!); bluff of the barranca near Guadalajara, Sept. 14, 1891, *C. G. Pringle* 5154 (GH!). *Pringle* 5154 is chosen as the lectotype because it is more complete. The name was published in a paper concerning plants discovered by Pringle, and this specimen is annotated in what appears to be Robinson's writing.

The leaves of this variety exhibit considerable latitude in shape and lobing, but are always deeply lobed with the ultimate segments very narrow. The inflorescence is more elongate and broader than in the other varieties.

JALISCO: *Pringle* 4627, 9872 (GH, NY, US); *King* 3656 (MICH, NY, TEX, US); *McVaugh* 18603, 15094, 20280 (MICH); *Wilbur & Wilbur* 1996 (US).

9b. Pscalium peltigerum var. **hintonii** Pippen, var. nov. PLATE 9

Varietas peltigera foliis profunde lobatis, caule glabro, inflorescentia majore differt.

Plants to ca. 0.5 m. tall; stems hirsute with multicellular white hairs to 2 mm. long; blades of the basal leaves shallowly 9- to 11-angled but not lobed, the margin mucronate-toothed; upper cauline leaves similar to but smaller than the lower ones; inflorescence tightly corymbose, 10 cm. long and broad (those examined not mature).

HOLOTYPE: México; Carboneras, Toma, July 21, 1935, *G. B. Hinton et al.* 7966 (MICH!, isotype NY!).

DISTRIBUTION: Known only from the type collection.

The floral characters are similar to var. *peltigerum* and the plants have similar fleshy subterranean tubers. They differ in that the leaves are angulate, not deeply lobed, and the stem is hirsute. Field obser-

vations and study of future material may indicate that var. *hintonii* deserves specific rank, but for the present it is considered only as a variety.

9c. Psacalium peltigerum var. latilobum Pippen var. nov. PLATE 10

Varietas peltigera foliorum lobis longioribus quam latioribus, caule glabro differt.

Plants to ca. 0.5 m. tall; stems sparsely pubescent; blades of the basal leaves lobed less than one-half the distance to the center, the primary lobes 10 or 11, 5–7 cm. wide at the base and equally long, the lobes subdivided into 2 or 3 secondary lobes, obtusely triangular or deltoid, about as broad as long; margins of the lobes coarsely, triangular-toothed; inflorescence corymbose, tightly compact, ca. 9 cm. long and broad (inflorescence not fully matured).

HOLOTYPE: Guerrero; 1½ miles W. of Omiltemi, 7,800 ft., June 11, 1953, *T. W. McCorcle & C. M. Rowell, Jr.* 3453 (MICH, sheet 1!; isotype, sheet 2!).

DISTRIBUTION: Known only from the type collection.

10. Psacalium poculiferum (S. Wats.) Rydb. Bull. Torrey Bot. Club 51:375. 1924.

Slender herbs ca. 1 m. tall; roots exuding a reddish-orange sap when cut; stems 4–7 mm. thick at the base, densely puberulent proximally becoming subglabrous upward and again puberulent in the inflorescence; leaves glabrous or sparsely puberulent mostly along the veins with 6- to 10-celled hairs ca. 0.5 mm. long; basal leaves 2 or 3, long-petioled, centrally or subcentrally peltate, subcircular in outline, 15–25 (–60) cm. in diameter; blades lobed one-third to two-thirds the distance to the depressed center, the primary lobes 7 or 8 (–10), 4–8 cm. wide at the base, usually 2–3 cm. longer than broad, each divided into 2 or 3 secondary lobes or merely triangulate, the margins irregularly toothed; petioles 15–30 (–40) cm. long, terete, slender, usually sparsely pubescent; cauline leaves 3 or 4, the lowermost similar in size and shape to the basal ones except the petiole leafy-margined and dilated at the base; cauline leaves progressively smaller upward; the uppermost bracteiform, nonpeltate, the petiolar portion leafy-margined, auriculate-based, the blade portion 5- to 7-lobed; inflorescence paniculate or corymbose, 12–30 cm. long and broad, the lower branches in the axils of the upper leaves; pedicels tomentose; calyculate bracts 3, subulate, about 1 mm. long (or lacking); heads about 100, 9–10 mm. long; phyllaries 3–5 (usually 4), varying on the same plant, elliptic or obovate, (4–) 5–6 (–7) mm. long, 1–3 mm. wide, glabrous, the tips purplish; flowers 3–5, opposite the phyllaries; corolla 6–8 mm. long, the tube as long as the lobes, 3–4 mm., the lobes linear, 0.5 mm. wide, the throat none; anthers 2–3 mm. long;

style branches ca. 1 mm. long, the tips truncate or rounded with a terminal or subterminal fringe of trichomes; mature achenes oblong or narrowly ellipsoid, 5 mm. long, 1–1.5 mm. wide, pubescent with fuscous, unicellular hairs; pappus (3.5–) 5–6 (–8) mm. long, creamy.

DISTRIBUTION: Western Jalisco to Nayarit, north to Sinaloa. Rocky, grass-oak dominated slopes and pastured areas. Flowering in mid-July and August.

This species is unusual because of the very small heads with mostly 4 phyllaries and flowers. It is closely related to *P. tabulare* but differs in its sparser pubescence and smaller heads. Both, however, have similar leafy, auriculate-based, cauline leaves.

JALISCO: *Pippen* 19, 21, 27, 60 (MICH); *Pringle* 9874, 4414 (GH, NY, US); *Wilbur & Wilbur* 2017, 2166 (MICH, US). NAYARIT: *Rose* 1935 (GH, US); *King* 3677 (MICH, NY, TEX, US); *Pippen* 11 (MICH); *McVaugh* 16406, 18838 (MICH). SINALOA: *Ortega* 7146 (US, the leaf of this specimen is somewhat atypical but this inflorescence is very similar to *P. poculiferum*).

11. Psacalium tabulare (Hemsl.) Rydb. Bull. Torrey Bot. Club 51:375. 1924.

Senecio tabularis Hemsl. Biol. Centr. Amer. Bot. 2:248. 1881. Holotype: Veracruz; valley of Orizaba, Escamella, Aug. 16, 1866, *Bourgeau* 2926 (K, not seen; isotypes GH! and C, Field Mus. Neg. 22631!).

Cacalia tabularis (Hemsl.) A. Gray, Proc. Amer. Acad. 19:52. 1883.

Plants up to 2 m. tall (*Balls* 5350); stems at least 7 mm. thick at the base, purplish, densely pubescent; leaves sparsely pubescent on the adaxial surface, densely pubescent on the abaxial surface, the hairs multicellular, 1–1.5 mm. long, 15- to 20-celled; basal leaves 2–4, long-petioled, peltate, subcircular in outline, 16–27 (–60, *Balls* 5350) cm. in diameter, the venation radiate with 8 principal veins; blades lobed about half way to the center, the primary lobes 7 or 8, 5–8 cm. long and broad, each usually divided into 3 triangular secondary lobes, 1–2.5 cm. long, 2–3 cm. broad, the margins coarsely deltoid-toothed; petioles up to 35 cm. long, terete, pubescent; cauline leaves 2–4; the lowermost subcentrally peltate, the blades broadly ovate or subcircular, 14–16 cm. long, 15–17 cm. wide, palmately 6- to 7-lobed, the petioles attached to the blade about 3 cm. above the base, leafy-margined, auriculate-based; uppermost cauline leaves sessile, auriculate-based, 3-lobed distally; inflorescence paniculate, 30–40 cm. long, 8–30 cm. broad, the branches often sparsely stipitate glandular, subtended by narrowly triangular bracts 1–5 cm. long, 0.3–1 cm. wide; pedicels 5–10 mm. long, with 2–5 subulate bracts, 2–6 mm. long; heads 75 to over 100, about 12 mm. long; phyllaries 5, narrowly ovate, 9–10 mm. long, 2–3 mm. broad, mostly glabrous or occasionally sparsely pubescent; receptacle 1.5 mm. across; flowers 5, opposite the phyllaries; corolla 7–9 mm. long, the tube (3.5–) 4–5 mm. long, the throat campanulate 0.5–1 mm. long and wide, the lobes 3 mm. long, linear; anthers 3 mm. long; style branches 1–1.5 mm. long, hispid on the abaxial

surface, the tips truncate or obtuse with a terminal or subterminal fringe of trichomes; mature achenes narrowly ellipsoid, 5–5.5 mm. long, 1.5 mm. wide, 1 mm. or less thick, glabrous, pale, about 18-ribbed; pappus (5.5–) 6–7 mm. long, white.

DISTRIBUTION: Known mostly from western Veracruz and eastern Puebla and one specimen collected in Michoacán. Openings in oak-pine woodlands. Flowering from August to October.

This species is very closely related to *P. poculiferum*, but differs in that the heads always have 5 phyllaries and flowers, and glabrous achenes.

Some of the specimens examined are sparsely stipitate-glandular on the inflorescence branches but this is not constant in this species.

PUEBLA: *Purpus* 5630 (GH, NY, US). MICHOACÁN: *Pippen* 55 (MICH). VERACRUZ: *Balls* 5350 (US); *Muller* s.n., August 1843 (NY); *Sharp* 44823 (NY).

12. Psacalium species

Plants to about 1 m. tall; stems slender, to 5 mm. thick at the base, subscapose, densely hirsute below with white, nonglandular multicellular hairs up to 1 mm. long, distally sparsely hirsute with nonglandular hairs as well as minutely stipitate glandular; leaves glabrous on the adaxial surface, sparsely pubescent along the veins on the abaxial surface; basal leaves 2 or 3, long-petioled, peltate, subcircular in outline, 20–30 cm. across, venation radiate with about 8 principal veins; blades lobed one-third to one-fourth (rarely one-half) the distance to the center of the blade, the primary lobes 6 or 7, 5–8 cm. wide at the base about as long as wide, each usually divided into 3, triangular attenuate-tipped secondary lobes; petioles slender, to 30 cm. long, pubescent; cauline leaves 1 (or 2), similar to the basal leaves but much smaller; inflorescence paniculate, ca. 35 cm. long, 25 cm. broad, the branches densely stipitate-glandular, subtended by petiolate, leafy bracts, the blade to 6 cm. long, elliptic, entire or palmately 3- to 5-lobed; pedicels purple, to 3 cm. long; calyculate bracts 3–7, subulate, 4–5 mm. long; heads few, immature; phyllaries (7 or) 8, oblong or elliptic, ca. 10 mm. long, 2–3 mm. wide, hirsute, occasionally sparsely glandular; flowers ca. 9, achenes glabrous; pappus white, chromosome number, $n=30$ (Turner, ined.).

DISTRIBUTION: Known only from Guerrero. Flowering probably in November.

These specimens appear to be somewhat intermediate between *Psacalium eriocarpum* and *P. holwayanum*. They differ from both of these species by the glabrous achenes, the leafy inflorescence bracts, the mostly glabrous basal leaves, as well as the distinct geographical range.

These specimens probably represent either a distinct species or a variety of one of the above. The material examined was immature

and could not be studied thoroughly. Perhaps after future collections have been studied and field observations made it will be possible to assign a name.

GUERRERO: *McVaugh* 21913* (MICH); *Sharp* 441496 (NY).

Doubtful Names and Excluded Taxa

Cacalia albicans Sessé & Moc. Fl. Mex. ed. 2. 180. 1894. Known only from the type description. This cannot be associated with any species of the genera discussed in this paper. According to the description the leaves are lanceolate and sinuately pinnatifid and therefore this probably should be referred to *Senecio*.

Cacalia amplexicaulis Schultz Bip. ex Klatt, Leopoldina 24:125, in synonymy, 1888. Listed as a synonym of *Senecio bracteatus* Klatt.

Cacalia berlandieri DC. Prod. 6:328. 1838. =**Senecio desortum** Hemsl. (Biol. Centr. Amer. Bot. 2:239. 1881).

Cacalia calotricha S. F. Blake, Contr. Gray Herb. II. 52:58. 1917. This should be referred to *Senecio*. The structure of the corolla is similar to that of *S. angulifolius* in that the throat is longer than the recurved lobes. The plant is apparently a shrub. It is known only from the type.

Cacalia eriopoda Schultz Bip. ex Klatt, Leopoldina 24:125, in synonymy, 1888. Listed as synonym of *Senecio eriopodus* Klatt.

Cacalia guatemalensis Standl. & Steyermark, Publ. Field Mus. Bot. 23:99. 1944. This should probably be referred to *Senecio* sect. *Mulgedifolii* since the description states that the flowers are purple and the inflorescence is glandular pubescent. This species is not a *Psacalium*, as suggested by Cuatrecasas (Brittonia 8:157. 1955) since, according to the description, the leaves are not peltate.

Cacalia incana Sessé & Moc. Pl. N. Hisp. ed. 1. 132. 1889. A later homonym of *C. incana* L., 1753.

Cacalia liebmannii Schultz Bip. ex Klatt, Leopoldina 24:125, in synonymy, 1888. Listed as a synonym of *Senecio liebmannii* Buchinger.

Cacalia lyrata Sessé & Moc. Pl. N. Hisp. ed. 1. 131. 1889. Known only from the type description. This is probably referable to *Senecio* sect. *Mulgedifolii* because, according to the description, the flowers are purple and the leaves are lyrate-pinnatifid.

Cacalia macrophylla Sessé & Moc. Pl. N. Hisp. ed. 1. 132. 1889. Later homonym of *Cacalia macrophylla* Bieb. 1808.

Cacalia pallescens Schultz Bip. ex Klatt, Leopoldina 24:126, in synonymy, 1888. Listed as a synonym of *Senecio pallescens* Klatt. Rydberg transferred this species to *Odontotrichum* based on a tracing in Klatt's herbarium.

Cacalia parasitica Schultz Bip. Bot. Zeit. 15:759. 1857. According to Greenman (Contr. U.S. Nat. Herb. 23:1635. 1924) this is *Senecio parasiticus* Greenm. It is a shrub. No specimens have been seen by me.

Cacalia peltata Sessé & Moc. Pl. N. Hisp. ed. 1. 132. 1889. A later homonym of *Cacalia peltata* H.B.K. [*Psacalium peltatum* (H.B.K.) Cass.]

Cacalia pinnatifida Sessé & Moc. Pl. N. Hisp. ed. 1. 132. 1889. A later homonym of *C. pinnatifida* L., 1767. The description and photograph of the type (an illustration) indicate that this is probably *Odontotrichum amplifolium* (DC.) Rydb.

Cacalia prenanthoides H.B.K. Nov. Gen. et Sp. 4:167. 1820. =**Erechtites valerianaefolia f. prenanthoides,** Belcher (Ann. Mo. Bot. Gard. 43:30. 1956).

Cacalia purpurascens Schultz Bip. ex Klatt, Leopoldina 24:126, in synonymy, 1888. Listed as a synonym of *Senecio purpurascens* Klatt.

Cacalia pudica Standl. & Steyermark, Publ. Field Mus. Bot. 23:255. 1947. This is not in any of the genera herein considered, because the flowers are purple and the throat of the corolla is much longer than the lobes. It is more closely related to *Senecio* Sect. *Mulgedifolii.*

Cacalia runcinata H.B.K. Nov. Gen. et Sp. 4:168. 1820. =**Senecio roseus** Schultz Bip. (Flora 28:498. 1845).

Cacalia runcinata Less. Linnaea 5:162. 1830. =**Senecio coulteri** Greenm. (Ann. Mo. Bot. Gard. 1:272. 1914).

Cacalia sarracenica Sessé & Moc. Fl. Mex. ed. 2. 180. 1894. A later homonym of *Cacalia sarracenica* L., 1753.

Cacalia sinuata Sessé & Moc. Pl. N. Hisp. ed. 1. 1889. A later homonym of *Cacalia sinuata* Cerv. 1824 [*Odontotrichum sinuatum* (Cerv.) Rydb.].

Cacalia spathulata Sessé & Moc. ex D. Don, Trans. Linn. Soc. 16:250. 1833. =**Chaptalia nutans** (according to Blake).

Cacalia subdecurrens Schulz Bip. ex Klatt, Leopoldina 24:125, in synonymy, 1888. Listed as a synonym of *Senecio deformis* Klatt.

Cacalia suffulta Greenm. Proc. Amer. Acad. 32:310. 1897. This probably should be referred to *Senecio.* It is not a member of the genera herein discussed, because the flowers are bright orange, the throat of the corolla is longer than the lobes, and the achenes have hygroscopic trichomes.

Cacalia tepicana M. E. Jones, Contr. West. Bot. 15:156. 1929. =**Senecio hartwegii** Benth. according to Blake (Contr. U.S. Nat. Herb. 29:136. 1945).

Cacalia toluccana DC. Prod. 6:328. 1838. =**Senecio callosus** Schultz Bip. according to Greenman (Ann. Mo. Bot. Gard. 1:271. 1914).

Cacalia tuberosa Sessé & Moc. Pl. N. Hisp. ed. 1. 132. 1889. A later homonym of *Cacalia tuberosa* Nutt. 1818.

Cacalia viscosa Sessé & Moc. Pl. N. Hisp. ed. 1. 132. 1889. Known only from the type description which states that it is a shrub; therefore, it is most probably not a species in the genera discussed in this paper.

Odontotrichum delphinifolium Rydb. Bull. Torrey Bot. Club 51:419. 1924. Rydberg saw only the type specimen which was in fruit. This species has since been collected in flower. It is not an *Odontotrichum,* because the inflorescence has only one large head, yellow radiate flowers, and no pappus. This taxon should probably be referred to the *Heleneae.*

Odontotrichum liebmannii (Buchinger) Rydb. Bull. Torrey Bot. Club. 51:419. 1924. Rydberg transferred this species from *Senecio* on the strength of a tracing of a leaf in the Klatt Herbarium at the Gray Herbarium. I have seen no specimens and cannot associate the description or the tracing of Klatt's with any species of the genera of this paper (see *C. liebmannii* Schultz Bip. above).

Psacalium thyrsoideum DC. Prod. 6:335. 1838. Known only from the type description. It was questionably published by DeCandolle as a *Psacalium*. Thus far the description has not been matched with any other cacalioid species. The type specimen is probably in Prague and must be examined before the position of this taxon can be determined.

Collections Cited Excluding Types

(Abbreviations: D.=Digitacalia; O.=Odontotrichum; Pe.=Pericalia; Ps.=Psacalium.)

ARSÈNE, G.

s.n. Nov. 1908, Ps. megaphyllum
s.n. Sept. 9, 1909, D. jatrophoides
s.n. Nov. 4, 1909, Pe. sessilifolia
s.n. Sept. 14, 1911, Pe. sessilifolia
93. O. sinuatum
93a. O. sinuatum
334. O. sinuatum
1181. O. sinuatum
2386. Ps. megaphyllum
5132. O. palmeri
5729. Pe. sessilifolia
5740. O. sinuatum
7347. Pe. sessilifolia

ARSÈNE, G., & NICOLAS, BRO.

334. Ps. megaphyllum

BALLS, EDWARD K.

5299. Ps. peltatum v. peltatum
5333. O. amplifolium
5350. Ps. tabulare
5428. O. tussilaginoides
5575. Pe. sessilifolia

BARCLAY

s.n. O. pringlei

BARKLEY, FRED A.

14A624. O. decompositum

BEAMAN, JOHN

3619. Ps. peltatum v. peltatum

BLUMER, J. C.

1378. O. decompositum

BOURGEAU

715. Pe. sessilifolia
716. O. sinuatum
2926. Ps. tabulare

CAMP, W. H.

2401. Ps. peltatum v. conzattii

CONZATTI, C.

715. D. heteroidea
4015. O. purpusii

CONZATTI, C., & GONZALEZ, V.

397. O. amplifolium
1237. O. purpusii

DARROW, R.

s.n. July 4, 1937, O. decompositum

DARROW, R., PHILLIPS, & PULTZ

1235. O. decompositum

DODDS, DONALD, & SIMPSON, ROBT. F.

32. Pe. michoacana

DIGUET, L.

s.n. July 1912, O. palmeri

DUGES, A.

451. O. sinuatum
481. Pe. sessilifolia

EGGLESTON, W. W.

10765. O. decompositum

FEDDEMA, CHARLES

10. O. sinuatum
161. Pe. sessilifolia
183. O. palmeri
308. O. palmeri
381. Pe. sessilifolia
1345. Pe. sessilifolia

FERRIS, ROXANA S.

5881. O. pringlei

GALEOTTI, H.

2491 bis. O. cirsiifolium

GENTRY, HOWARD S.

536M. O. decompositum
1959. O. decompositum

2815. O. decompositum
6968. Pe. sessilifolia
6969. O. pachyphyllum
8562. O. sinuatum

GENTRY, HOWARD S., CORRELL, & ARGUELLES

18016. Ps. peltatum v. peltatum

GHIESBREGHT

805. O. cirsiifolium

GILLY, C. L., SR.

5. Ps. holwayanum

GOLDMAN, E. A.

132. O. sinuatum

GODDING, L. N.

s.n. Aug. 28, 1912, O. decompositum
784. O. decompositum

GOULD, FRANK W.

8989. O. sinuatum

GRAHAM, SHIRLEY

94. O. sinuatum
99. O. globosum
100. O. radulifolia
124. O. palmeri

HARTWEG

125. O. sinuatum

HEWITT, W. P.

68. O. decompositum

HINTON, G. B.

1266. O. goldsmithii v. goldsmithii
1908. Ps. peltatum v. peltatum
2200. Ps. megaphyllum
2355. Ps. megaphyllum
2487. Ps. holwayanum
2755. Pe. michoacana
4993. Pe. michoacana
7984. O. goldsmithii v. goldsmithii
8066. O. goldsmithii v. goldsmithii
8211. O. cirsiifolium
8349. O. amplifolium
9202. O. goldsmithii v. goldsmithii
9436. O. cirsiifolium
12146. O. brachycomum
12572. D. napeifolia
12718. Pe. michoacana
13463. O. amplifolium
13469. Pe. michoacana
13480. Ps. megaphyllum
14464. Ps. nanum
14877. Ps. peltatum v. peltatum
15078. O. goldsmithii v. goldsmithii
15288. O. brachycomum
15624. O. brachycomum
15629. Ps. megaphyllum

IBARRA GRACIA, P.

407. O. globosum
414. Ps. peltatum v. peltatum

JONES, MARCUS E.

25053. O. decompositum
27692. O. pringlei

JONY, P.

s.n. in 1892. O. platylepis

KEARNY, T. H., & HARRISON, G. J.

6045. O. decompositum
6194. O. decompositum

KEARNY, T. H., & PEEBLES

10092. O. decompositum

KENOYER, L. A.

2110. O. radulifolium
2330. O. radulifolium

KING, ROBERT M.

3615. O. silphiifolium
3656. Ps. peltigerum v. peltigerum
3659. O. palmeri
3677. Ps. poculiferum
6737. O. sinuatum

KING, ROBERT M., & SODERSTROM, T. R.

4904. O. brachycomum

KNOBLOCH, I. W.

1273. O. globosum
1293. O. decompositum

KRUCKEBERG, A. R.

4644. O. decompositum

LEAVENWORTH, WM. C.

539. O. palmeri

LESUEUR, HARDE

145. O. decompositum

LYONNET, E.

194. Pe. sessilifolia
794. Ps. peltatum v. peltatum
3122. Ps. peltatum v. peltatum

MANNING, W. E. & M. S.

53560. O. radulifolium

MATUDA, E.

19148. O. silphiifolium
19417. O. silphiifolium
19706. O. sinuatum
21808. O. sinuatum
21825. Pe. sessilifolia
26175. Ps. peltatum v. peltatum
26572. Ps. megaphyllum
26632. Ps. peltatum v. peltatum
26882. O. sinuatum
27730. O. amplifolium
28343. Ps. peltatum v. peltatum
28821. O. cirsiifolium
29313. O. amplifolium
29483. Ps. peltatum v. peltatum
29591. Ps. peltatum v. peltatum
29609. O. amplifolium
29787. Pe. sessilifolium
30015. Ps. holwayanum

MAYSILLES, JAMES

7579. Pe. sessilifolia
7587. O. radulifolium
7752. O. sinuatum
7755. Pe. sessilifolia
7784. O. pachyphyllum
7793. O. sinuatum
7880. O. sinuatum
8448. O. sinuatum
8485. O. sinuatum

MCVAUGH, ROGERS

12810. O. sinuatum
12929. O. palmeri
13321. Ps. megaphyllum
13559. Pe. sessilifolia
13616. O. pringlei
13625. Pe. sessilifolia
13684. Ps. eriocarpum
13821. Ps. peltatum v. peltatum
14093. Pe. michoacana
14136. Pe. michoacana
14165. Ps. eriocarpum
14287. Ps. eriocarpum
14290. Pe. michoacana
14390. Pe. michoacana
15094. Ps. peltigerum v. peltigerum
15313. O. cervinum
15460. O. goldsmithii v. goldsmithii
16132. O. goldsmithii v. goldsmithii
16406. Ps. poculiferum
17118. Pe. sessilifolium
17160. D. jatrophoides
17183. Pe. sessilifolia
17650. Ps. megaphyllum
17726. O. amplum
18121. Pe. sessilifolia
18603. Ps. peltigerum v. peltigerum
18838. Ps. poculiferum
20280. Ps. peltigerum v. peltigerum
20481. O. palmeri
21355. Pe. michoacana
21658. Pe. sessilifolia
21659. O. pachyphyllum
21729. O. pachyphyllum
21731. O. pachyphyllum
21732. O. globosum
21733. O. sinuatum
21734–39. O. globosum x O. sinuatum
21765. O. pringlei
21823. D. napeifolia
21824. O. amplifolium
21826. Ps. peltatum v. conzattii
21897. Ps. megaphyllum
21903. D. tridactylitis
21910. Ps. megaphyllum
21928. Ps. megaphyllum
21934. O. brachycomum
21953. Ps. holwayanum
21960. O. palmeri
21964. O. brachycomum

MCVAUGH, R., & KOELZ, W.

39. Ps. megaphyllum
48. O. platylepis
49. O. sinuatum
57. O. amplum
147. Pe. sessilifolia
276. O. sinuatum
435. Pe. michoacana
441. O. palmeri
479. Pe. sessilifolia
601. O. pringlei
656. Pe. sessilifolia

792. Pe. sessilifolia
919. Ps. eriocarpum
920. Pe. sessilifolia
1104. O. pringlei
1253. O. pringlei

MEXIA, YNEZ

635. Pe. sessilifolia
845. O. pringlei
877. Ps. megaphyllum
1450. Pe. sessilifolia
1656. Pe. michoacana

MEARNS, EDGAR A.

531. O. decompositum
2219. O. decompositum

MEYER, F. G., and ROGERS, D. J.

2608. O. radulifolium

MICKEL, JOHN T.

501. O. radulifolium
561. O. radulifolium

MOORE, H. E., JR.

3421. O. silphiifolium
5119. Ps. megaphyllum

MOORE, H. E., JR. & CETTO, M.

5469. Pe. michoacana

MULLER, C. H.

3420. O. decompositum

MÜLLER, F.

s.n. in 1853. Ps. tabulare
1619. O. silphiifolium

NARVAEZ MONETS, M., & SALAZAR, A. E.

557. O. platylepis

NELSON, E. W.

1061. O. amplifolium
1133. D. napeifolia
1420. O. cirsiifolium
2080. D. tridactylitis
2243. O. amplifolium
3117. O. cirsiifolium
3467. D. chiapensis
4758. O. decompositum
4759. O. globosum
4954. Ps. peltatum v. peltatum
6582. Ps. peltatum v. peltatum

OWNBEY, GERALD B., & OWNBEY, FINDLEY

1874. O. pachyphyllum

ORCUTT, C. R.

3746. O. silphiifolium

ORTEGA, JESUS G.

5727. Pe. sessilifolia
7146. Ps. poculiferum

PALMER, EDWARD

s.n. July 1890. O. decompositum
s.n. 1892. O. pringlei
47. Pe. sessilifolia
168. O. palmeri
576. Pe. sessilifolia
651. O. sinuatum
689. O. platylepis
1234. O. pringlei
1832. Pe. sessilifolia

PARRY & PALMER

541. Pe. sessilifolia
543. O. radulifolium
543. Ps. peltatum v. peltatum

PENNELL, FRANCIS W.

18332. O. pachyphyllum
18343. Ps. peltatum v. peltatum
18345. Pe. sessilifolia
18582. O. globosum

PHILLIPS, EDWIN A.

651. O. decompositum

PIPPEN, RICHARD W.

1. O. sinuatum
2. O. amplum
3. O. amplum
4. O. amplum
5. Pe. sessilifolium
6. Ps. peltatum v. peltatum
7. O. sinuatum
8. Ps. megaphyllum
9. O. sinuatum
10. O. palmeri
11. Ps. poculiferum
12. O. palmeri
13. Pe. sessilifolia
15. Pe. sessilifolia
16. Ps. megaphyllum
17. Pe. sessilifolia
18. Pe. sessilifolia
19. Ps. poculiferum
20. O. palmeri
21. Ps. poculiferum
22. O. sinuatum
23. O. platylepis

24. Ps. megaphyllum
25. O. multilobum
26. Pe. michoacana
27a. O. palmeri
27. Ps. poculiferum
28. O. palmeri
29. O. cf. palmeri
30. O. multilobum
31. Pe. sessilifolia
32. O. palmeri
33. Pe. sessilifolia
34. Pe. sessilifolia
36. Ps. eriocarpum
37. O. pringlei
38. Pe. michoacana
39. Ps. megaphyllum
40. O. multilobum
43. O. palmeri
44. Ps. peltatum v. peltatum
45. O. sinuatum
46. D. jatrophoides
47. Ps. megaphyllum
48. Pe. sessilifolia
49. Ps. peltatum v. peltatum
50. O. sinuatum
51. Pe. sessilifolia
52. O. cirsiifolium
53. Ps. peltatum v. peltatum
54. O. silphiifolium
56. O. sinuatum
57. O. sinuatum
58. O. platylepis
59. O. pringlei
60. Ps. poculiferum
61. Pe. sessilifolia
62. Ps. eriocarpum
63. Pe. michoacana
64. Pe. sessilifolia
65. Pe. michoacana
66. Ps. eriocarpum
67. Ps. eriocarpum

POWELL, A. M., & EDMONDSON, J.

869. O. palmeri
929. O. radulifolium
948. O. sinuatum

PRINGLE, C. G.

767. O. decompositum
1736. Pe. sessilifolia
1811. O. pringlei
1816. O. platylepis
2304. O. palmeri
3340. Ps. peltatum v. peltatum
3566. O. radulifolium
4095. O. radulifolium
4262. D. jatrophoides
4274. O. sinuatum
4414. Ps. poculiferum
4672. Ps. peltigerum v. peltigerum
4778. D. napeifolia
4785. O. amplifolium
4984. O. cirsiifolium
5272. O. cirsiifolium
5741. D. jatrophoides
6018. O. paucicapitatum
6164. D. tridactylitis
6165. Ps. megaphyllum
6176. D. heteroidea
6238. Ps. peltatum v. conzattii
6453. O. silphiifolium
7983. Pe. sessilifolia
9080. O. silphiifolium
9868. Ps. tussilaginoides
9869. Pe. sessilifolia
9870. Ps. peltatum v. peltatum
9871. Ps. peltatum v. peltatum
9872. Ps. peltigerum v. peltigerum
9873. O. platylepis
9874. Ps. poculiferum
9875. O. sinuatum
9877. D. tridactylitis
10024. O. napellifolium
10117. Pe. michoacana
10126. O. brachycomum
11497. Pe. sessilifolia
11499. O. pringlei
11500. O. palmeri
13297. Ps. holwayanum
13672. Ps. holwayanum
13979. Ps. holwayanum

PURPUS, CARL A.

3038. Ps. peltatum v. peltatum
3139. O. amplifolium
3845. O. purpusii
4113. Ps. calvum
5625. Pe. sessilifolia
5630. Ps. tabulare

ROSE, J. N.

1935. Ps. poculiferum
1986. O. cervinum
2101. O. filicifolium
2248. cf. O. palmeri
2337. Ps. laxiflorum

2828. Pe. sessilifolia
3040. D. jatrophoides
3471. O. globosum x O. sinuatum
3575. O. amplum
7808. O. sinuatum

ROSE, J. N., & HAY, ROBERT

5311. O. silphiifolium
5547. O. tussilaginoides

ROSE, J. N., & PAINTER, J. H.

6738. O. tussilaginoides
7939. Ps. peltatum v. peltatum

ROSE, J. N., ET AL.

9187. O. silphiifolium

ROWELL, CHESTER M., JR.

3387. O. goldsmithii v. rowellii
3604. O. goldsmithii v. rowellii
3779. O. napellifolium
3886. O. goldsmithii v. rowellii
3896. O. napellifolium

RZEDOWSKI, J.

15974. O. amplifolium
16015. O. amplifolium
16073. O. goldsmithii v. rowellii

SAFFORD, WILLIAM E.

1432. O. platylepis
1451. Pe. sessilifolia

SALAZAR, F.

s.n. Aug. 1, 1913. O. napellifolium

SCHAFFNER, J. G.

s.n. Sept. 1955. Pe. sessilifolia
255. Pe. sessilifolia
294. O. radulifolium
294. Ps. peltatum v. peltatum

SCHUMANN, W.

148. O. radulifolium

SEATON, HENRY

s.n. in 1891. Ps. peltatum v. peltatum

SEEMANN

s.n. O. pachyphyllum

SELER, ED.

1259. Ps. peltatum v. peltatum

SHARP, A. J.

44508. Ps. peltatum v. peltatum
441431. O. goldsmithii v. rowellii
441465. O. amplifolium

SHREVE, FORREST

8031. O. globosum

SMITH, CHARLES L.

287. D. heteroidea
380. D. tridactylitis
387. D. heteroidea
388. D. jatrophoides

SMITH, LUCIUS C.

123. D. jatrophoides
124. O. amplifolium
966. D. tridactylitis

SMYTH, E. G.

172. O. sinuatum

STANFORD, RETHERFORD, & NORTHCRAFT

818. O. radulifolium

STANFORD, TAYLOR, & LAUBER

2421. O. radulifolium
2535. Ps. peltatum v. adenophorum

TOWNSEND, C. H. T.

s.n. in 1909. O. decompositum

TOWNSEND, C. H. T., & BARBER, C. M.

158. O. decompositum

TUCKER, J. M.

2456. O. decompositum

VISCHER

14. Pe. sessilifolia
58. O. sinuatum

WATERFALL, U. T.

12668. O. pachyphyllum

WHITE, STEPHEN S.

2741. O. decompositum
3289. O. decompositum
4353. O. decompositum

WILBUR, R. L. & C. R.

2017. Ps. poculiferum
2166. Ps. poculiferum

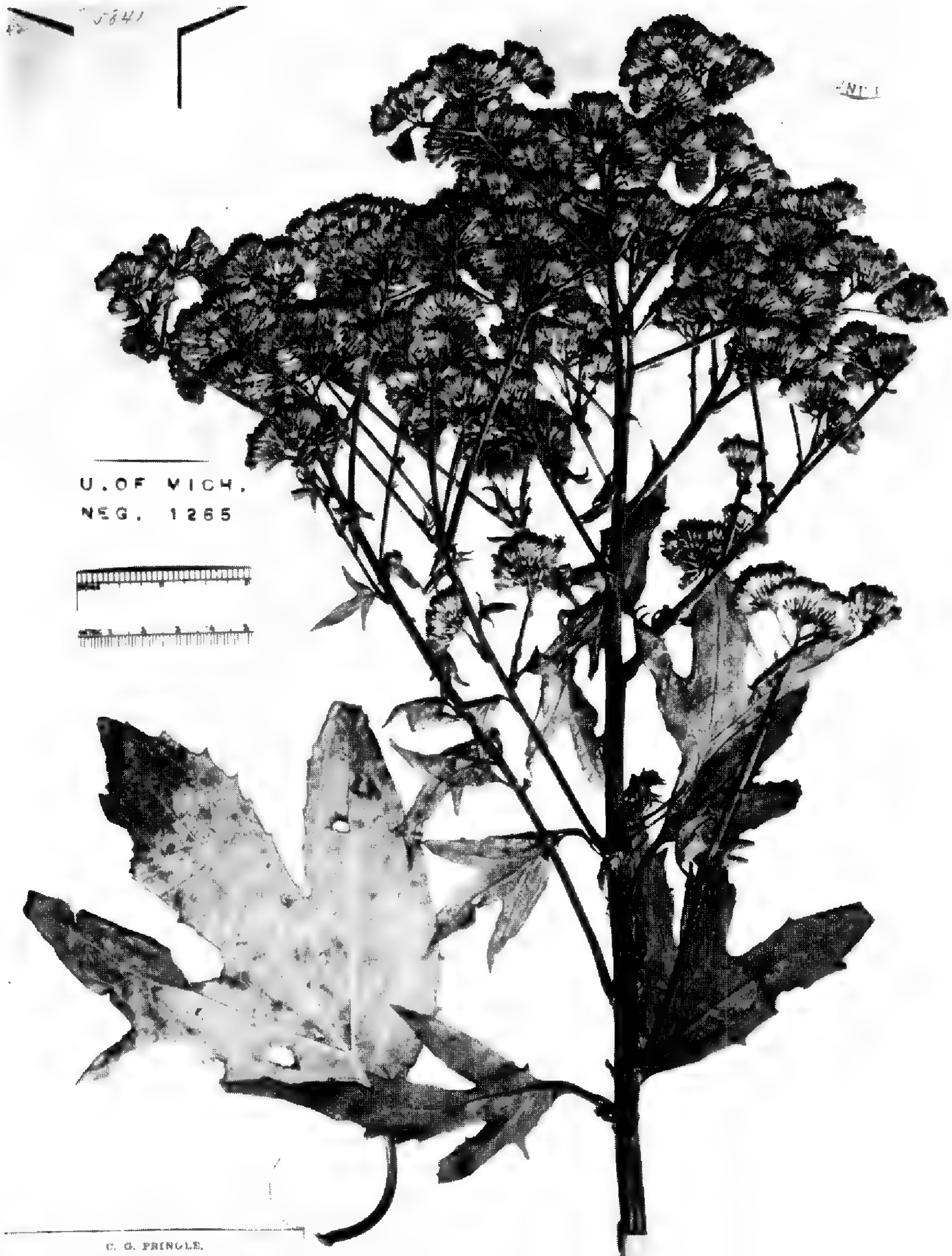
WILCOX, TIMOTHY E.

s.n. in 1891. O. decompositum

WRIGHT, CHARLES

1286. O. decompositum

PLATES



Digitacalia tridactylitis (Rob. & Greenm.) Pippen (type, *Pringle* 5841, GH).

JUN 12 1962

Odontotrichum goldsmithii var. *rowellii* Pippen, var. nov. (type, *Rowell* 2991, MICH).

APR 27 19

U. OF MICH.
NEG. 1228

Odontotrichum pringlei (S. Wats.) Rydb. (lectotype, *Pringle* 1749, GH).

Pericalia michoacana (B. L. Rob.) Rydb. (type, *Pringle* 10117, GH).

U. OF MICH.
NEG. 1283

2490 Cacalia peltata, HBK.

Psacalium megaphyllum (Rob. & Greenm.) Rydb. (type, *Pringle* 2090, GH).

Psacalium nanum Pippen, sp. nov. (type, *Hinton* 14464, US).

Enlargement of *Psacalium nanum* Pippen, sp. nov. (type, *Hinton* 14464, US).

Psacalium peltigerum var. *hintonii* Pippen, var. nov. (type, *Hinton* 7966, MICH).

Psacalium peltigerum var. *latilobum* Pippen, var. nov. (type, *McCorcle* and *Rowell* 3453, MICH).

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THE LICHEN GENERA CETRELIA AND PLATISMATIA (PARMELIACEAE)

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and CHICITA F. CULBERSON

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THE LICHEN GENERA CETRELIA AND PLATISMATIA (PARMELIACEAE)

By William Louis Culberson
and Chicita F. Culberson

Introduction

In 1960 we undertook a monographic study of the old genus *Cetraria* in the traditionally broad sense that it was understood in Zahlbruckner's *Catalogus Lichenum Universalis*. It soon became obvious that this assemblage contained several major constellations of species and that these species groups were not particularly closely related to each other. One of these major groups is of course *Cetraria* itself, and this genus will be the subject of a future publication. A small, homogeneous, arctic-alpine segregate genus named *Asahinea* has already been treated (Culberson and Culberson, 1965). Two groups remain—the new segregate genera *Platismatia* and *Cetrelia*. The aim of the present study is to describe and delimit these genera and to present a comprehensive treatment of the species which belong to them.

This study has the additional objective of examining the nature of chemical variation in morphologically well defined species groups. It was obvious early in our research that the plants under study showed chemical variations strikingly correlated with morphologic ones. Moreover, the chemical compounds themselves seemed to have closer relationships to each other than those previously noted in other genera of approximately the same size. We decided, therefore, to treat chemistry and morphology in equal detail in our study. Of course, the use of chemistry in lichen taxonomy is now so commonplace that it is impossible to imagine a serious treatment of any group showing chemical diversity in which this aspect of the variation was left unstudied. Few lichenologists, however, have tried to integrate chemical and morphological data or to place chemical variation in the same evolutionary frame of reference in which critical taxonomy places morphological variation. But if we are to involve chemistry in taxonomy, an attempt, however crude, must be made to delineate the nature of chemical variation in lichens. In this monograph we present two genera to serve as subjects for the kind of

theoretical speculation that will lead eventually to the structuring of a framework of principles upon which practical taxonomic judgments can rest.

Historical Background

From the very beginning, generic concepts have been one of the most unsatisfactory aspects of the taxonomy of lichenized fungi. Linnaeus, in his *Species Plantarum* of 1753, considered all the species as members of the single genus *Lichen* and, to the detriment of lichenology, the insensitive Linnaean treatment was selected as the starting point for the nomenclature of the whole group. Even Acharius, the first botanist to see the lichens with a discerning and critical eye, began by keeping all the species in the genus *Lichen* (Acharius, 1798), obviously simply in deference to tradition. A few years later though, in 1803, he divided the lichens into some two dozen genera, one of them being *Cetraria*.

As originally described, the genus *Cetraria* contained eight species, namely:

C. islandica (L.) Ach.
C. cucullata (Bell.) Ach.
C. nivalis (L.) Ach.
C. lacunosa Ach.
C. fallax (L.) Ach.
C. glauca (L.) Ach.
C. sepincola (Ehrh.) Ach.
C. juniperina (L.) Ach.

The genus soon became a general repository for all parmeliaceous plants with marginal or submarginal apothecia. It was used in its Acharian sense for the species listed above and for related species by most of the major lichenological authors of the nineteenth century, for example, Schaerer, Fries, Tuckerman, Körber, and Massalongo. Nylander alone among the leading lichen students of the time arranged the species differently. He took up the almost forgotten genus *Platisma* described by Hoffmann in 1790—although he changed the spelling to "*Platysma*"—and used it to classify all but one of Acharius' *Cetrariae* (Nylander, 1855). In so doing, he effectively typified the genus *Cetraria* Ach. with *Lichen islandicus* L. by leaving only that species in it (Culberson, 1966b). Nylander's revival of *Platysma* reflected his belief that *Cetraria*, as conceived by other botanists of the time, was not homogeneous.

Although all these species had marginal or submarginal apothecia and pycnidia, it was difficult to find any other major traits shared by even the restricted list of species that Acharius originally put into the genus. In the original complement of species listed above, Nylander saw the erect, linear-lobed, subfruticose, soil-inhabiting *Cetraria islandica* as an element too foreign from the other more distinctly foliose species to be classified in the same genus with them. Nylander, however, apparently did not question the generic affinity of all the foliose species that he recognized in *Platysma*. He saw no obstacle to

classifying the broad-lobed, *Parmelia*-like *Cetraria glauca* and the narrow-lobed, erect, soil-inhabiting species such as the familiar *C. cucullata* and *C. nivalis* in the same genus.

As time passed, other workers described many more species in *Cetraria*, and the generic concept became more nebulous still. There were species with marginal, reflexed apothecia, such as *Cetraria stracheyi* Bab., that in some later classifications were transferred to the genus *Nephromopsis* Müll. Arg. There was also a whole array of very broad-lobed forms, most of them foreign to Europe and superficially resembling the *Amphigymnia* Parmelias, for example *Cetraria sanguinea*, *C. collata*, and *C. japonica* from the Orient. In addition, a few particularly anomalous species, such as *C. chrysantha* Tuck. and *C. thomsonii* Stirt., were put in *Cetraria* in spite of their lacking any connection whatever with the bulk of the species already classified there, except for having marginal apothecia.

The *Catalogus Lichenum Universalis* (Zahlbruckner, 1930) took a particularly broad view of *Cetraria* and included all the plants mentioned above and most of their obvious relatives, excluding only a few of the species as members of the genus *Nephromopsis*. Zahlbruckner's *Catalogus* had the effect of rigidly formalizing these generic concepts. With the exception of this study, subsequent treatments have either followed him in recognizing *Cetraria* and *Nephromopsis* (Räsänen, 1952) or have taken a still more conservative position and recognized only *Cetraria* (Rassadina, 1950). Only Eilif Dahl tried to evaluate the major variations among the plants that had been referred to *Cetraria* and to define the major natural groups in an assemblage of species that years of casual taxonomy had left biologically meaningless.

The "Parmelioid" *Cetrariae*

Dahl challenged the monophyletic nature of *Cetraria* sens. lat. He pointed out that *Cetraria glauca* (L.) Ach., *C. norvegica* (Lynge) Du Rietz, *C. collata* Müll. Arg., and *C. chrysantha* Tuck. differed from the true Cetrarias both morphologically and chemically. The cortex in these species, he demonstrated, is composed of densely agglutinated hyphae with tiny lumina, a type of cortex that he called "platysmoid" but which is more commonly called prosoplectenchymatous (Ozenda, 1963). The upper cortex of true Cetrarias, on the other hand, is composed of thin-walled hyphae with inflated lumina, a type generally termed paraplectenchymatous. These anatomical differences were correlated with the distribution of some lichen substances. The dozen true Cetrarias that Dahl analyzed chemically were characterized by a predominance of usnic acid and fatty acids while the species with a prosoplectenchymatous cortex were characterized by a predominance of atranorin. On the basis of this morphological and chemical information, Dahl postulated that *Cetraria* sens. lat. was polyphyletic. He

segregated the species with the prosoplectenchymatous upper cortex and the presence of the substance atranorin from the true Cetrarias and used the old genus *Platisma* Hoffm. to accommodate them.

When we started our study of the lichens traditionally assigned to *Cetraria*, we made a preliminary survey to determine the general range of the morphological and the chemical variation. It was soon obvious that the difference that Dahl had pointed out between the "true" Cetrarias and the members of the *Cetraria glauca* group was indeed a basic one, and it held up as even more and more species were considered. We thereupon decided to put aside the true Cetrarias and to study first the broad-lobed species that had traditionally been classified with them, a group which for convenient reference we can call the "parmelioid" *Cetrariae*.

The "parmelioid" *Cetrariae* include the *Cetraria glauca* group as well as such species as *C. sanguinea*, *C. japonica*, and *C. collata*. These latter Asiatic species all have pseudocyphellae, a trait present in some but not all members of the *C. glauca* group. Although the position of *C. sanguinea* and *C. japonica*, for example, had never been seriously disputed, apparently no one had noticed that these species were extremely closely related to other species that have always been considered Parmelias, for example *Parmelia cetrarioides* and *P. olivetorum*. (But the superficial similarity of *P. cetrarioides* Del. to the Cetrarias was pointed out from the very beginning by Delise in his choice of the specific epithet.) A species which several years ago was (erroneously) being called *Cetraria collata* in North America is so similar to *Parmelia cetrarioides* that the two species can be separated from each other with certainty only by chemical tests. Although we were unsure of the taxonomic disposition which should be made of all these species, it was clear that *P. cetrarioides* and *P. olivetorum* were very closely related to at least some of the "parmelioid" *Cetrariae* and that they should be classified with them and not among the true *Parmeliae*.

Our knowledge of the "parmelioid" *Cetrariae* was summed up when we compared these plants, the true Cetrarias, and the *Amphigymnia* Parmelias to three very peculiar, distinctive, and closely related species which had been classified in *Cetraria* and which we defined as the new genus *Asahinea* (Culberson and Culberson, 1965). The traits of the "parmelioid" *Cetrariae* and the three other species groups were summarized then in a form which we present here with only slight modifications (Table 1).

But the "parmelioid" *Cetrariae* are themselves not a homogeneous group. From the outset it was clear that the bulk of the "parmelioid" *Cetrariae* really consists of two distinct constellations of species rather than of a single spectrum of forms. Although from Dahl's treatment we might have expected these species to be characterized by the presence of fatty acids as the medullary lichen substances, only some of the

TABLE 1.—*A comparison of the Major traits in* Parmelia *sect.* Amphigymnia, Asahinea, *the "parmelioid"* Cetrariae (=Cetrelia+Platismatia), *and* Cetraria *sens. str.*

	Parmelia sect. *Amphigymnia* (106 species)	*Asahinea* (3 species)	"Parmelioid" *Cetrariae* (24 species)	*Cetraria* sens. str. (about 75 species)
Cortex	prosoplecten-chymatous	prosoplecten-chymatous	prosoplecten-chymatous	paraplecten-chymatous
Rhizines	present	absent	present	present in most
Marginal ciliae	present in many	absent	absent	present in some
Pycnidia	laminal	laminal or marginal	marginal	marginal
Apothecia	laminal	laminal or marginal	laminal or submarginal	marginal
Disc	perforate in many	imperforate	perforate in most	imperforate
Lichen substances	many; aromatic and aliphatic	4 aromatic	many; aromatic and aliphatic	many; aromatic and aliphatic
Distribution	nearly worldwide	Northern Hemisphere, arctic-montane	Northern Hemisphere, mainly temperate	Northern Hemisphere, arctic-temperate

species were actually found to contain fatty acids. More than half the species produced (as medullary constituents) one or more aromatic compounds, orcinol-type depsides (anziaic, imbricaric, microphyllinic, olivetoric, and perlatolic acids), or orcinol-type depsidones (alectoronic and α-collatolic acids). All the species producing aromatic compounds exclusively as the medullary substances belong to the "*Parmelia cetrarioides*" group while those producing a fatty acid (invariably caperatic acid) as the medullary constituent all belong to the "*Cetraria glauca*" group. The chemistry of the species of the two groups is summarized in Table 2. An analysis of the chemical relationships of the compounds in each group is given in a discussion farther on.

The two groups into which the species fall by similarity of general habit as well as by chemistry of the medullary substances are marked by suites of additional morphological and chemical traits (Table 3). Internally, each of the two groups of the "parmelioid" *Cetrariae* is extremely uniform and yet each is so distinct from the other that they cannot be considered congeneric. We propose the genus *Platismatia* for the 10 members of the *Cetraria glauca* group and *Cetrelia* for the 14 members of the *Parmelia cetrarioides* group.

As characterized here, the genera *Cetrelia* and *Platismatia* both show relatively conservative variation and extremely high levels of internal homogeneity. The chemical variation here is far more precisely cor-

TABLE 2.—*The distribution of the constant chemical substances in the species of* Cetrelia *and* Platismatia *and the number of specimens tested of each species. The few unidentified "accessory" substances found are not tabulated*

	atranorin	caperatic	alectoronic	anziaic	α-collatolic	fumarprotocetraric	imbricaric	microphyllinic	olivetoric	perlatolic	Number tested
CETRELIA											
alaskana	+						+				14
braunsiana	+		+		+						32
cetrarioides sens. str.	+									+	35
cetrarioides sens. lat.	+						+				34
chicitae	+		+		+						24
collata	+						+				17
davidiana	+								+		7
delavayana	+									+	8
isidiata	+			+							4
japonica	+							+			22
nuda	+		+		+						22
olivetorum	+								+		19
pseudolivetorum	+								+		31
sanguinea	+			+							67
sinensis	+						+				6
PLATISMATIA											
erosa	+	+									17
formosana	+	+									2
glauca	+	+									11
herrei	+	+									5
interrupta	+	+									20
lacunosa	+	+					+				8
norvegica	+	+									7
regenerans	+	+									4
stenophylla	+	+									5
tuckermanii	+	+									7

related with visible traits (Table 3) than in most genera of the macrolichens. All the species of *Platismatia* produce the aliphatic fatty acid caperatic acid as the medullary constituent and only one species produces a β-orcinol-type depsidone (fumarprotocetraric acid) in addition to the aliphatic substance. The species of *Cetrelia*, on the other hand, never produce fatty acids as the medullary constituents but only aromatic substances—orcinol-type depsides and depsidones, substances all rather closely related to each other chemically.

One might wonder whether the genera *Cetrelia* and *Platismatia*, as

TABLE 3.—*A comparison of the major traits in* Platismatia *and* Cetrelia, *the two genera constituting the "parmelioid"* Cetrariae

Cetrelia (= the *Parmelia cetrarioides* group)	*Platismatia* (= the *Cetraria glauca* group)
Upper surface always pseudocyphellate	Upper surface usually pseudocyphellate
Soredia rare	Soredia common
Isidia common	Isidia rare
Lobulae absent	Lobulae common
Upper cortex always IKI−	Upper cortex often IKI+
Subhymenium thick, IKI−	Subhymenium thin, IKI+
Thick zone of algae usually present immediately below subhymenium	Algae usually absent from immediately below subhymenium
Spores large, ellipsoid, 11–22 × 6–12μ	Spores small, subspherical, 5–8 × 3–5μ
Pycnidia common in most species	Pycnidia rare in most species
Pycnoconidia with inflated ends	Pycnoconidia without inflated ends
Medullarly chemistry: substances all aromatic orcinol-type depsides and depsidones	Medullary chemistry: the aliphatic substance caperatic acid in every species (one species also with a depsidone)
14 species	10 species
Greatest species concentration in eastern and southeastern Asia	Greatest species concentration in the amphi-North Pacific

delimited by the morphological and chemical criteria explained above, show phytogeographically meaningful distributional patterns, since such distributions are expected in monophyletic genera. While many parts of the world remain inadequately explored lichenologically, the plants that we are concerned with here are large and conspicuous and have often been collected, even by amateur plant hunters. Their general conspicuousness and the frequency of their collection give one a confidence in the significance of maps of their distribution that one would not have for smaller, less noticeable cryptogams. In Figure 1 the number of species of *Cetrelia* and of *Platismatia* in floras in various parts of the world is plotted. It is obvious from these maps that the genera have very different centers of maximum species numbers although both genera are circumpolar. *Platismatia* is represented most abundantly in the amphi-North Pacific, especially western North America. *Cetrelia*, on the other hand, is most richly represented in East and Southeast Asia. From this phytogeographic evidence it would seem indisputable that *Cetrelia* and *Platismatia* had different centers of origin. It is also noteworthy that neither genus is represented in Australia or New Zealand. *Cetrelia* is not present in Africa, and *Platismatia* is represented there only by a few isolated mountain stations for the ubiquitous *Platismatia glauca*. The genus *Cetraria* (in the strict sense) likewise does not exist in Africa but *Parmelia* sect. *Amphigymnia* (Hale, 1965) is richly represented there. *Cetrelia* is also absent from South America, and *Platismatia* is repre-

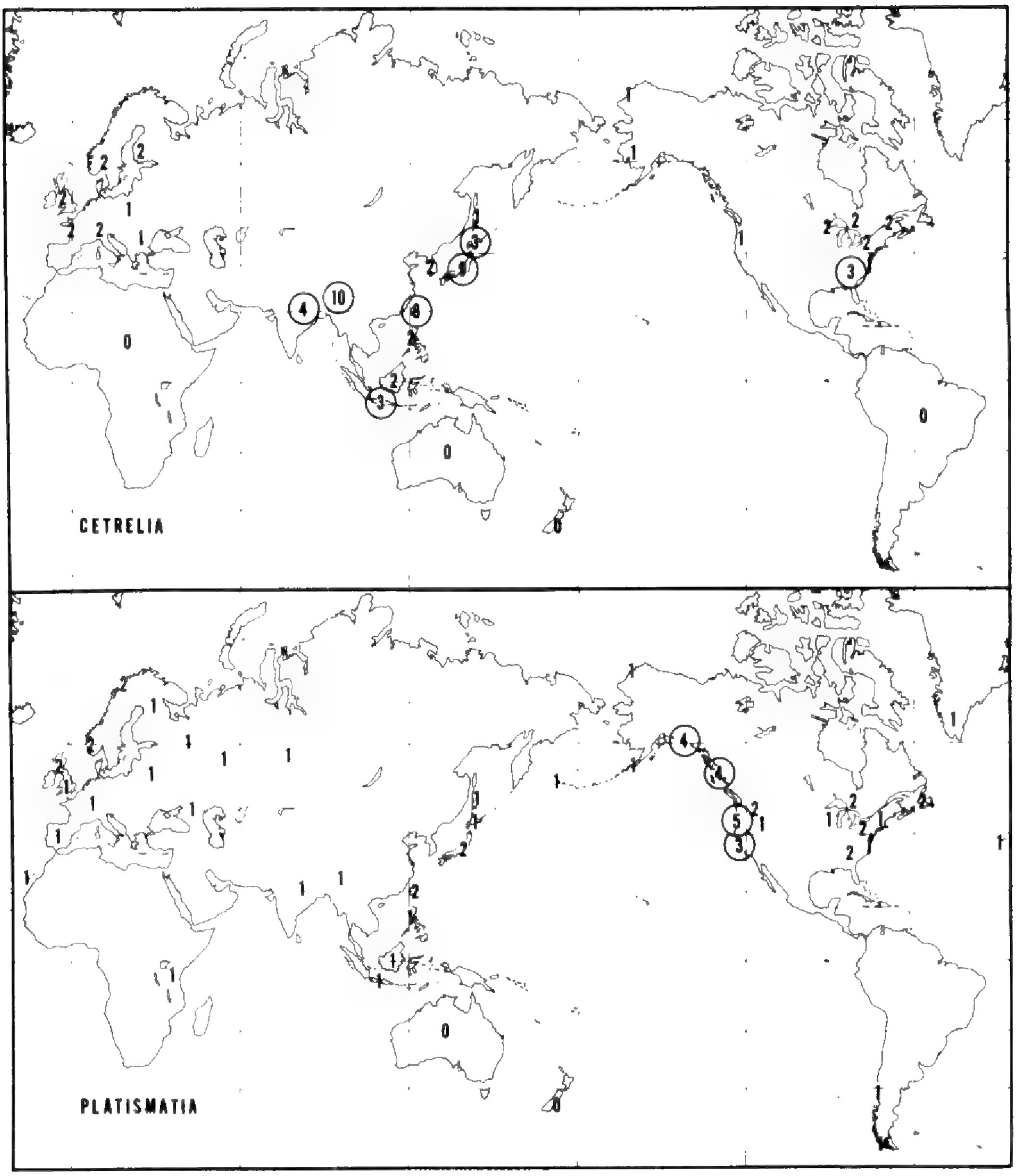

FIGURE 1. The distribution of the genera *Cetrelia* (above) and *Platismatia* (below) by numbers of species in floras in various parts of the world.

sented only in the southern part of that continent and there again by *P. glauca* alone. Both *Cetrelia* and *Platismatia* are temperate, Northern Hemisphere genera, but their different centers of origin and overall ranges clearly indicate that the distinctive morphological and chemical traits that characterize them are the product of different and independent evolutionary histories.

Morphology

The following morphological characteristics have proved to be the most useful in the study of the species of the genera *Cetrelia* and *Platismatia:*

CORTEX

The genera of macrolichens, with a few exceptions such as *Collema*, have a true cortex. The cortex is recognizable as the outermost part of the thallus and shows a greater range of anatomical variation than any other vegetative tissue. It may consist of hyphae that are essentially free, erect, and at right angles to the surface of the thallus (e.g., *Roccella*), or interwoven and parallel to the surface of the thallus (e.g., *Anaptychia*), or densely agglutinated throughout. If the hyphae are agglutinated, they may be either inflated and have large lumina (paraplectenchyma)—as in *Peltigera*, *Leptogium*, or *Sticta*—or they may be very little if at all inflated and have tiny lumina (prosoplectenchyma)—as in *Ramalina* and *Parmelia*. The various cortex types have been summarized by Ozenda (1963). In general the major cortex variations closely follow generic lines and the members of a single genus generally all tend to show the same cortex type.

Dahl (1952) pointed out that the species of true *Cetrariae* which he studied have a paraplectenchymatous cortex and that the species which he assigned to the genus *Platysma* have a prosoplectenchymatous cortex. This distinction between the true *Cetrariae* and the so-called "parmelioid" *Cetrariae* has held up even after all the known species have been examined. It is a basic difference of fundamental importance between the "parmelioid" *Cetrariae*—the genera *Platismatia* (Plate 8, Figures 43–44), *Cetrelia* (Plate 8, Figure 42), and *Asahinea* (Plate 7, Figure 40)—and the true *Cetrariae* (Plate 7, Figures 37–38). In its anatomy, the upper cortex of *Cetrelia* and *Platismatia* is very similar to that of the species of *Parmelia* sect. *Amphigymnia* (Plate 7, Figure 39) and indeed to that of the whole genus *Parmelia*, it would seem, although a detailed study of cortex structure throughout *Parmelia* has never been made. The importance of cortex anatomy in defining the "parmelioid" *Cetrariae* as distinct from *Cetraria* is so great that these species would be considered isolated from *Cetraria* even without the accompanying, correlated evidence based upon morphology and chemistry (Table 1). But the fact that *Cetrelia* and *Platismatia* actually have a large series of other traits separating them from the true *Cetrariae* merely underlines the basic and deep-seated nature of their taxonomic isolation from *Cetraria*.

Although cortex structure clearly separates *Cetraria* sens. str. from *Platismatia*, *Cetrelia*, and *Asahinea*, it shows no variations of major consequence among these three genera. The upper cortex in *Platismatia* and *Cetrelia* ranges from about 15 to 30μ thick and the lower cortex from about 10 to 30μ thick. The lower cortex of these genera bears rhizines here and there although naked areas may be extensive. In producing rhizines from the lower cortex these genera differ strik-

ingly from *Asahinea* which does not (Culberson and Culberson, 1965). In addition, although not strictly a cortex trait, a reddish-purple pigment is also generally produced in the lower part of the medulla in *Asahinea*, especially in moribund zones near the lower cortex. It is notable that such pigmentation never occurs in *Cetrelia* or *Platismatia*.

PSEUDOCYPHELLAE

Pseudocyphellae are small pores in the cortex through which, if they are big enough, the medulla is directly visible. The upper cortex of all the species of *Cetrelia* and of about half the species of *Platismatia* is pseudocyphellate.

In *Cetrelia* there are two kinds of pseudocyphellae, the small type (Plate 12, Figure 52) and the large type (Plate 12, Figure 73). Most species have pseudocyphellae of the small type. These little apertures are less than a millimeter wide and punctiform or irregular in shape. *Cetrelia cetrarioides*, *C. chicitae*, and *C. braunsiana*, for example, all have small pseudocyphellae. Large pseudocyphellae, found in *C. nuda* and *C. collata*, exceed one millimeter in width and often appear to result from the confluence of smaller pores. In the species producing large pseudocyphellae, many specimens show at least some pseudocyphellae of the small type as well.

The distinction between small and large pseudocyphellae was especially valuable in distinguishing *Cetrelia chicitae* and *C. nuda* in Japan. Table 5, under the treatment for *C. braunsiana* (p. 495), shows the distribution of pseudocyphellae of these two types as compared to the distribution of other morphological traits among these three related species in Japan.

PUNCTA

Perforations found in the lower cortex of some of the species may have distinct taxonomic significance. These pores may not all be of similar origin, and those in *Platismatia* appear to be somewhat different from those in *Cetrelia*. To stress the fact that the exact nature of these peculiar pores or spots in the lower cortex is not clear, we call them puncta rather than pseudocyphellae.

Puncta are best developed in the lower cortex of *Platismatia erosa* (Plate 11, Figure 51) and *P. formosana* where they furnish a valuable trait for distinguishing the former species from the closely related *P. interrupta* and the latter species from the morphologically somewhat similar species *P. lacunosa*. Other members of *Platismatia* lack these conspicuous interruptions in the lower cortex altogether.

A number of species of *Cetrelia* also shows similar spotlike modifications of the lower cortex. The species of *Cetrelia* which produce puncta

do not do so invariably, however, and in this genus the tendency to produce a punctate lower cortex has little taxonomic value. *Cetrelia cetrarioides*, *C. collata*, *C. davidiana*, and *C. isidiata* all consist of individuals that show at least some puncta in the lower cortex and others that do not, and the occurrence or absence of the trait does not seem to be correlated with any other variations. On the other hand, some *Cetrelia* species—for example *C. alaskana*, *C. braunsiana*, and *C. sanguinea*—never produce a punctate lower cortex.

In *Cetrelia* some of the puncta are actual pores in the lower cortex and are apparently equivalent to the well developed ones seen in some species of *Platismatia*. But in *Cetrelia* the lower cortex may also show pale flecklike spots and every intergradation between these spots and the true punctate pores. It may be that puncta originate as spots and finally become an actual hole in the lower cortex. In general, though, the abundance of the spots is greater in individuals of such species as *Cetrelia cetrarioides* than is the abundance of true perforations.

In examining the lower cortex of *Cetrelia* species for puncta, one often sees tiny holes in the cortex that are wounds which were made when the specimen was removed from its substrate. Careful observation will distinguish such irregular, sharp-edged wounds from the punctate pores and the associated spotting discussed above, both of which are entirely natural attributes of the plants. Puncta in the lower cortex of *Parmelia* (=*Cetrelia*) *olivetorum* and *P. cetrarioides* were observed by Gyelnik (1933), who was so impressed by these "pseudocyphellae" that he described two new species, *Pseudoparmelia aradensis* and *P. pseudofallax*, based upon them. A year later he (Gyelnik, 1934) reduced *Pseudoparmelia pseudofallax* to a form of *Parmelia* (=*Cetrelia*) *cetrarioides* after he discovered that these "pseudocyphellae" were common and widespread in the latter species. Later still, in a study of the putative genus *Pseudoparmelia*, Santesson (1942) showed that the "pseudocyphellae" in *Pseudoparmelia cyphellata* Lynge, the only species in the genus prior to Gyelnik's two additions, were nothing but wounds where the lower cortex had been pulled off with the rhizines at the time of collection. Santesson assumed that the "pseudocyphellae" in the lower cortex of specimens assigned to this genus by Gyelnik were analogous to those which he described and illustrated in the South American species *P. cyphellata*. But from Gyelnik's descriptions it is clear that the "pseudocyphellae" which he saw in the European plants that he studied were puncta, as defined in the present study, and not wounds of casual origin.

ISIDIA

Isidia are rare in *Cetrelia* but relatively common in *Platismatia*. In *Cetrelia* only *C. braunsiana* (Plate 13, Figure 55) and *C. isidiata* are truly

isidiate. In both these species, however, some individuals are almost devoid of isidia altogether.

In an occasional plant of some ordinarily lobulate species, such as *C. pseudolivetorum* or *C. sinensis*, some of the thallus appendages or lobulae along the margins of the lobes may be so reduced in size that they do not show the dorsiventrality typical of lobulae but resemble isidia instead. These species should properly not be considered isidiate.

In the genus *Platismatia* the species *P. norvegica*, *P. erosa*, and *P. herrei* are regularly isidiate as are many individuals of the polymorphic *P. glauca*. Even in the habitually isidiate species, nonisidiate individuals are sufficiently common to be found with some regularity and, as one would guess, the extent of isidia production in isidiate individuals varies greatly. Also, in some sorediate species the soredia become consolidated into structures that are distinctly isidioid. *Platismatia interrupta* is a particularly variable species in which the soredia may become isidioid; some populations of *P. glauca* also show this tendency.

SOREDIA

Soredia are common in *Cetrelia* but relatively rare in *Platismatia*—essentially the reverse of the situation for isidia in these genera. The members of the *Cetrelia cetrarioides* group, with the single exception of *C. alaskana*, are all sorediate. The soredia are very fine and powdery and are produced, usually in abundance, at the edge of the lobes in continuous marginal soralia (Plate 13, Figure 54). The soralia are often so small that they can be seen easily only with some magnification.

In *Platismatia* there are no species in which soredia production is an invariable diagnostic trait. Soredia are produced, however, in some specimens of *P. glauca* and in many of *P. interrupta*. In these species the soredia often become isidioid, especially in the older parts of the thallus. In *Platismatia* the soredia are granular and laminal rather than minute and marginal as in *Cetrelia*.

It should be mentioned that an occasional specimen of certain species of *Platismatia*, such as *P. norvegica*, shows the development of conspicuous, capitate soralia on the upper surface of the lobes. Soralia of this sort are so infrequent yet so different from the ordinary soredia in both *Platismatia* and *Cetrelia* that they do not seem to be a normal thallus development at all. They are so anomalous that we regard them as a pathological abnormality and give them no taxonomic significance.

LOBULAE

Lobulae are minute, dorsiventral lobes on the upper surface and the margins of the thallus. In some specimens they are produced in such abundance on the surface of the thallus that the plants appear to be

cristate while in others they are more prominent on the margins so that the thallus appears to be elegantly fringed with tiny lobes. As we characterize them, lobulae are found in the genus *Cetrelia* but not in *Platismatia*. In *Cetrelia* they are restricted to the *C. japonica* complex of species, which includes *C. sinensis* and *C. pseudolivetorum* as well as *C. japonica* (Plate 17, Figure 63). Since both lobulae and isidia are similar in that they are entirely corticate and have an algal zone and a medulla, it is not surprising that they seem to intergrade in form in some specimens. In *C. pseudolivetorum*, for example, many of the lobulae produced are so small and narrow that they no longer show a distinct dorsiventrality and consequently closely resemble isidia. Since no entirely and truly isidiate race of *C. pseudolivetorum* is known, however, it would seem that the isidialike structures sometimes encountered in this species would better be interpreted as extremely reduced lobulae.

In *Platismatia* there are no structures analogous to the lobulae of *Cetrelia*. In fact, the only modified appendages produced at all are the special, branched, coralloid structures that develop from the expanded thallus lobes in some specimens of *Platismatia glauca* (Plate 21, Figure 70) and, more rarely, in *P. herrei*. These fruticose structures, however, are quite different from the tiny foliose lobulae produced by the species of *Cetrelia* discussed above.

APOTHECIA

In both *Cetrelia* and *Platismatia* the apothecia (Plate 10) are usually produced on the upper surface of the lobes and appear less frequently at the margins. In the position of the apothecia, both genera differ sharply from *Cetraria* in which the apothecia are strictly marginal.

With the exception of a few species, apothecial production in *Platismatia* is very infrequent. In *Cetrelia*, too, apothecia are very rare, except in the *C. collata* group. In both genera the infrequency of apothecial production contrasts strongly with the situation in *Cetraria* where apothecia are generally very common. The rarity of apothecia in the genera studied herein, however, recalls the *Amphigymnia* Parmelias in which the total lack or at least high infrequency of apothecia is typical of many species.

The only species of *Cetrelia* in which apothecia are produced with high regularity is the *collata* group—the species *C. sanguinea*, *C. davidiana*, *C. delavayana*, and *C. nuda*, in addition to *C. collata*. In Japan, 83 percent of the herbarium specimens of *C. nuda* were found to bear apothecia, and *C. sanguinea* in Java also often fruits. *Cetrelia collata*, *C. davidiana*, and *C. delavayana* are known in fruit, but these Chinese species have rarely been collected and the overall frequency of apothecia in them is impossible to assess.

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In the *Cetrelia cetrarioides* complex—including *C. cetrarioides*, *C. alaskana*, *C. isidiata*, *C. chicitae*, *C. olivetorum*, and perhaps *C. braunsiana*—only *C. chicitae* has been found in fruit with anything approaching commonness. In Japan about 17 percent of the plants are fertile, but in North America apothecial production in this species is much rarer. Although apothecia are known for *C. cetrarioides*, *C. olivetorum*, and *C. braunsiana*, they are very uncommon. In *C. cetrarioides*, in fact, only a single specimen bearing apothecia with apparently mature spores was seen in this study; and in *C. alaskana* and *C. isidiata* apothecia have never been observed at all.

In the *C. japonica* group, *C. japonica* and *C. pseudolivetorum* are very rarely known to fruit, while the other member of the complex, *C. sinensis*, has never been found with apothecia.

In *Platismatia*, apothecia are also very rarely produced, with two notable exceptions. The two North American species *P. tuckermanii* and *P. stenophylla* commonly fruit and almost every well developed specimen has apothecia. Two species, however, have never been found in fruit—*P. interrupta*, a common species in Japan, and *P. regenerans*, an apparent endemic of North Borneo. Apothecia in all the remaining six species of *Platismatia*—*P. erosa*, *P. formosana*, *P. glauca*, *P. herrei*, *P. lacunosa*, and *P. norvegica*—are known, but their occurrence is rare.

Many of the apothecia of both *Cetrelia* (Plate 11, Figure 50) and *Platismatia* become perforate, especially with age. In this trait they recall the species of *Parmelia* sect. *Amphigymnia* in which perforate apothecia are common. The true *Cetrariae*, however, have imperforate apothecia.

Internally, the apothecia of *Platismatia* and *Cetrelia* differ in a number of ways. In most species of *Platismatia* the subhymenium is in direct contact with the medulla while in *Cetrelia* a thick layer of algae separates the subhymenium from the medulla. The subhymenium of *Platismatia* and that of *Cetrelia* seem to differ markedly with regard to the products which make up the hyphal cell walls and, as a result, they also differ with regard to the color reactions that they exhibit with the IKI reagent. In *Cetrelia* the subhymenium remains uncolored in the presence of IKI, but in *Platismatia* it becomes some shade of purple, violet, lavender, or blue. There is, incidentally, no exception to this general difference. These reactions of the subhymenium, however, should not be confused with the dark blue reaction with IKI of the asci in the hymenium. This latter reaction is very widespread, probably universal, in both genera.

ASCOSPORES

Spores in the Parmeliaceae generally have been of very little systematic use. In *Platismatia* and *Cetrelia*, however, there is a very clear

distinction in the spores at the generic level. In *Platismatia* (Plate 9, Figure 46) the spores are small and short-ellipsoid, ranging in length from 5 to 8μ and in width from 3 to 5μ, with many of the spores being essentially subglobose. In *Cetrelia* (Plate 9, Figure 45), however, the spores are twice as large as those of *Platismatia* and range in length from 11 to 22μ and in width from 6 to 12μ. The large, more or less thick-walled spores of *Cetrelia* are very similar to those of the *Amphigymnia* Parmelias and less like the much smaller spores of the true Cetrarias.

PYCNIDIA

Like the apothecia, the pycnidia in the two genera are infrequent in general, only a very few species producing them with appreciable regularity. In *Cetrelia*, in fact, pycnidia are unknown altogether in five species, namely, *C. alaskana*, *C. cetrarioides*, *C. isidiata*, *C. olivetorum*, and *C. pseudolivetorum*. Pycnidia are known, but are infrequent to rare, in *C. braunsiana*, *C. chicitae*, *C. japonica*, and *C. sinensis*. Only in the *C. collata* complex do they appear to be common, although some of the Chinese species in this group—*C. collata*, *C. davidiana*, and *C. delavayana*—have been collected too infrequently to permit generalizations. *Cetrelia nuda* (Plate 10, Figure 49), the commonest member of this group in Japan, showed pycnidia in 100 percent of the specimens examined in Japanese herbaria. It will be recalled that it is precisely the *C. collata* complex, of which *C. nuda* is a member, which is the only segment of the genus *Cetrelia* regularly bearing apothecia. A high production of apothecia and a high production of pycnidia are very closely correlated in this group. Of course, the explanation could simply be that these species have a natural tendency to produce both these structures. Nevertheless, one is tempted to assume an intimate relationship in the close correlation of apothecia and pycnidia. If pycnidia and conidia (the pycniospores) which they produce were functioning here in sexual reproduction, then the high frequency of pycnidia in plants also bearing apothecia would be explained.

In *Platismatia* the situation is the same. The only two species in which pycnidial production is frequent are *Platismatia stenophylla* and *P. tuckermanii*. These are also the only two species of the entire genus which produce apothecia with great regularity. In *P. erosa*, *P. regenerans*, and *P. interrupta*, pycnidia are unknown altogether. *Platismatia interrupta* is noteworthy in this regard since it also has never been found with apothecia in spite of its being common in many parts of Japan. The other five species of *Platismatia*—*P. formosana*, *P. herrei*, *P. lacunosa*, *P. norvegica*, and *P. glauca*—all produce pycnidia very infrequently. Pycnidia are so rare in *P. glauca*, in fact, that none was seen in the hundreds of specimens of this common species examined in this study.

In both *Cetrelia* and *Platismatia* the pycnidia are produced on the margins of the lobes and not on the upper surface. In position, then, the pycnidia of both genera are similar to those of *Cetraria*.

The conidia in both genera are rod-shaped and small and measure about 1 by 4 to 5μ. Conidia in *Cetrelia* seem to be produced in the pycnidia with a higher frequency and in greater abundance than in *Platismatia* where pycnidia, seemingly without conidia, are more common. It also appears to be a consistent difference between the two genera that mature conidia in *Cetrelia* have inflated ends while those in *Platismatia* do not.

Chemistry

Of the ten substances identified in the species studied, a fatty acid (caperatic acid) and a β-orcinol-type depsidone (fumarprotocetraric acid) occur only in *Platismatia*, seven orcinol-type depsides and depsidones occur only in *Cetrelia*, and a β-orcinol-type depside (atranorin) is found in all species of both genera (Table 2). In this section an attempt will be made to suggest how these substances are related to each other. The discussion will be based primarily upon a comparison of the structures of these compounds in the light of what is known about biosynthetic pathways.

All the compounds involved here are derived from acetate and malonate units. An early branching point in the biosynthetic pathway (Figure 2) leads either to aliphatic compounds like the fatty acids or to aromatic substances like the phenolic acids. Phenolic acids may be

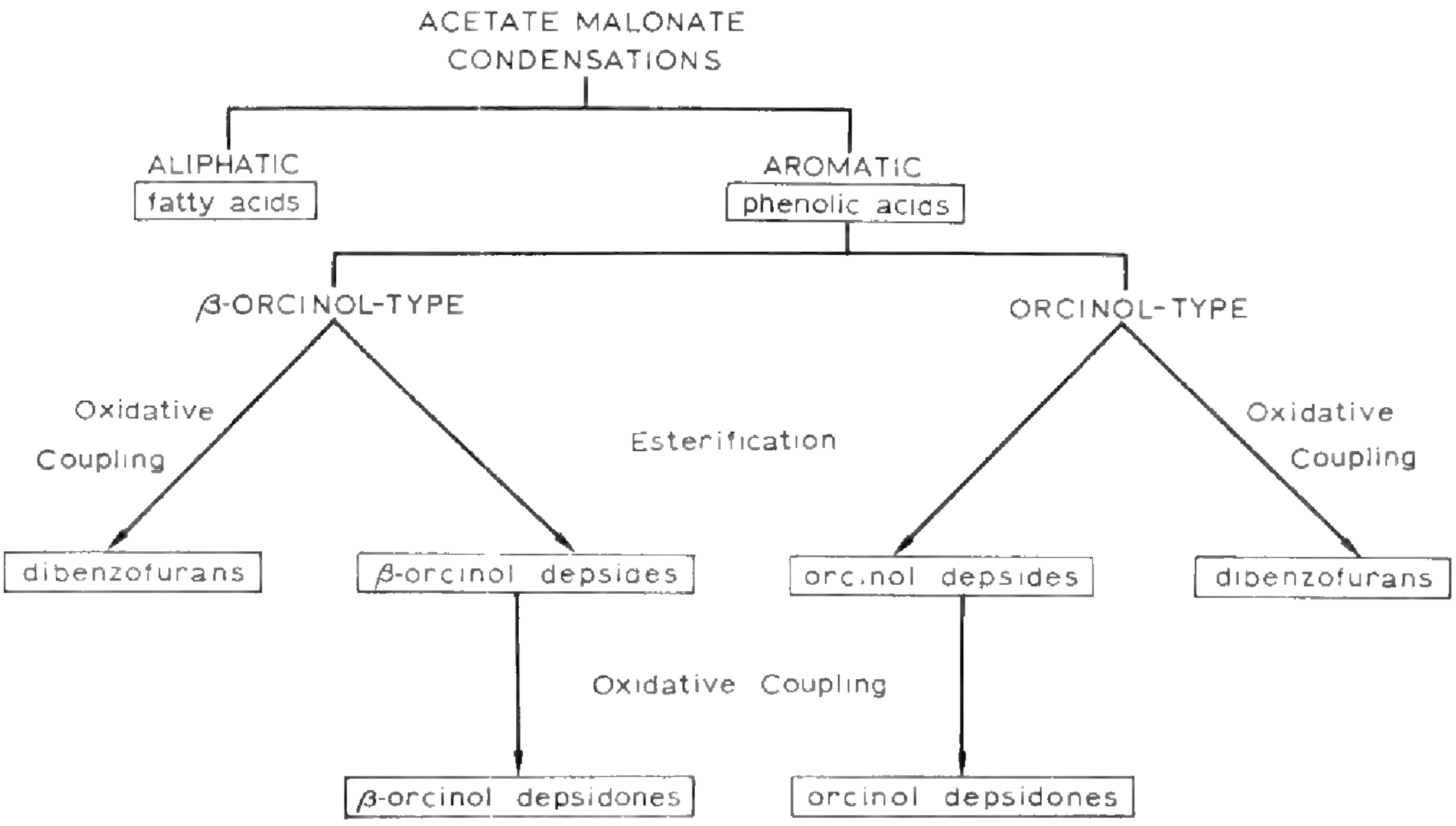


FIGURE 2. A generalized diagram showing postulated biosynthetic pathways in the elaboration of several major categories of taxonomically important lichen substances.

substituted by one of two patterns: namely, orcinol-type compounds like the medullary substances in *Cetrelia* or β-orcinol-type compounds like atranorin and fumarprotocetraric acid in *Platismatia*. Simple orcinol- and β-orcinol-type phenolic acids are esterified to depsides, and some depsides are cyclized to depsidones by oxidative coupling. They may also be methylated, chlorinated, hydroxylated, or decarboxylated (not shown in Figure 2). Various combinations of these relatively few reactions lead to most of the known lichen depsides and depsidones. Direct oxidative coupling of the phenolic acids can give dibenzofuran derivatives known from some species of lichens.

BIOSYNTHETIC DICHOTOMY LEADING TO AROMATIC AND ALIPHATIC SUBSTANCES

All the substances involved in this study appear to be of acetate-malonate origin (Shibata, 1965). Biosynthesis of fatty acids from acetate and malonate units has been the subject of very extensive studies showing formation of straight-chain aliphatic acids by linear condensations of malonate units after an initial condensation with an acetate unit (Richards and Hendrickson, 1964). Figure 3 presents a simplified version of the condensation of acetate and malonate units with reduction of the carbonyl groups to give a simple, saturated, fatty acid (left side of the figure). Caperatic acid has a slightly more complex structure, with three carboxyl groups (one as a methyl ester) and at least a superficial resemblance to citric acid.

Mosbach (1961, 1964) recently described the biosynthesis of the aromatic substance orsellinic acid from acetate and malonate units, but in this process an oxidized form of the chain of condensed units must undergo cyclization to produce the aromatic-ring system. Figure 3 also shows how one acetate and three malonate units could cyclize to orsellinic acid (right side of the figure). The carbonyl groups which are reduced during fatty-acid synthesis are required in aromatic synthesis to provide the double bonds in the aromatic ring—one of them by the loss of water in the cyclization step and two of them by enolization. Since the carbonyls are on alternate carbon atoms in acetate-malonate-derived carbon chains, *meta* orientation of phenolic groups is observed in the aromatic products.

ORCINOL- AND β-ORCINOL-TYPE SUBSTITUTIONS

An aromatic ring substituted with one alkyl group and two phenolic groups, such as orsellinic acid, is related to orcinol, and a ring with an additional carbon substituent *para* to the first is related to β-orcinol (Figure 4). Phenolic units in lichen substances are generally substituted according to one of these two systems. The biosnythetic origin

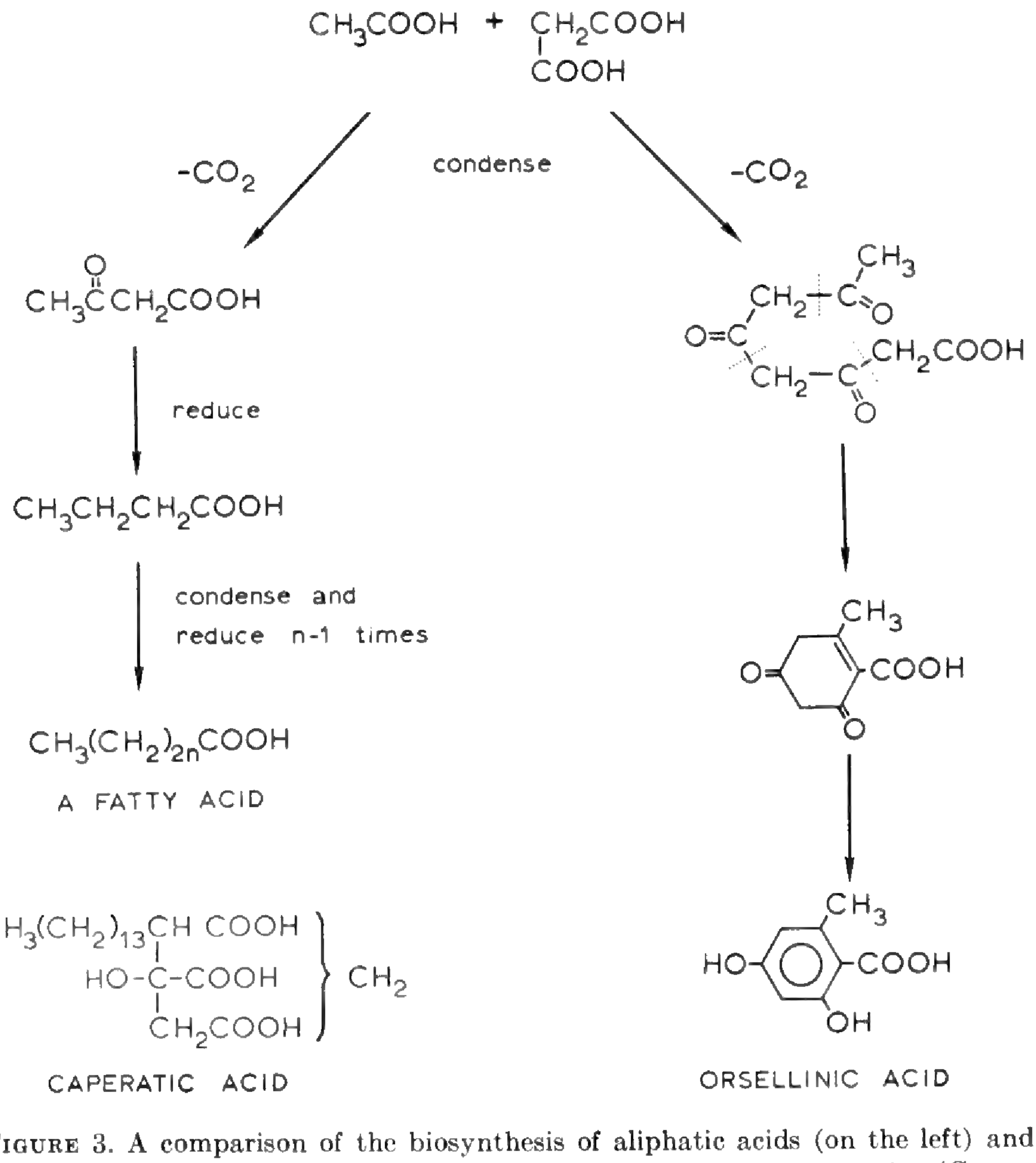
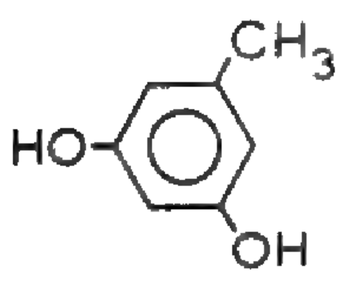


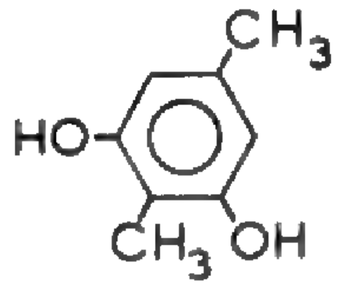
FIGURE 3. A comparison of the biosynthesis of aliphatic acids (on the left) and aromatic phenolic acids (on the right) from acetate and malonate units. (Caperatic acid, the medullary constituent of all species of *Platismatia*, is an example of a typical lichen fatty acid.)

of the extra carbon between the hydroxyl groups in β-orcinol systems is unknown.

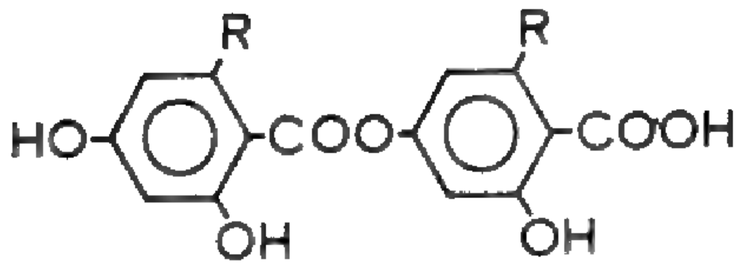
If the β-orcinol ring arises by direct carbon substitution onto a preformed orcinol-type ring, then β-orcinol substances would be derived from orsellinic acid by pathway "1" in Figure 4. For the complete synthesis of a depside such as atranorin, several more steps would be required including oxidation to an aldehyde and two esterification reactions. It is also possible to imagine a branched carbon chain which would produce the β-orcinol unit directly by cyclization (Figure 4, pathway "2"). Such a branched chain could form if a propionic acid unit replaced a malonic acid unit in the original condensation. Similar suggestions have been advanced to explain the synthesis of certain aromatic compounds occurring in other groups of plants (for



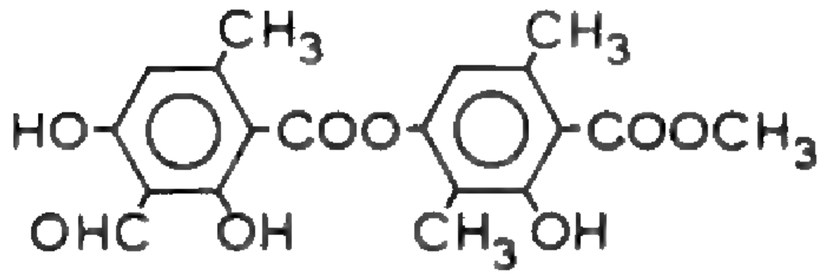
orcinol



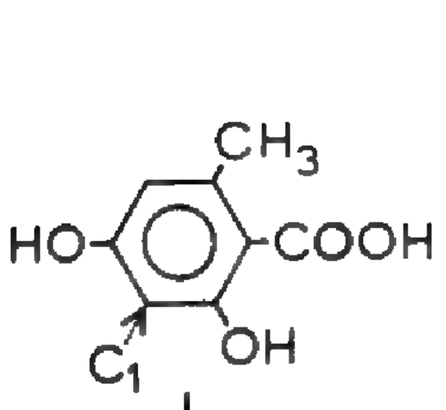
β-orcinol

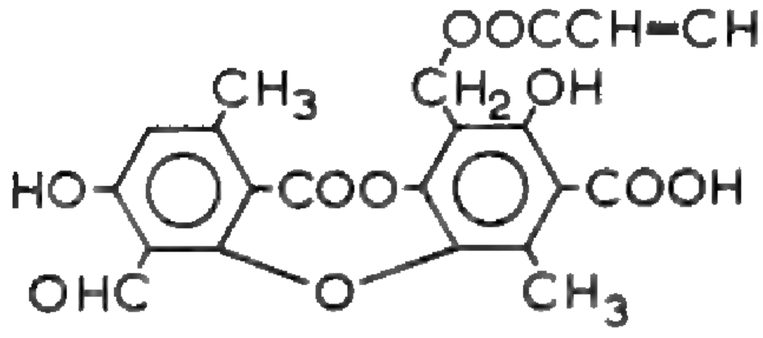


orcinol-type depside

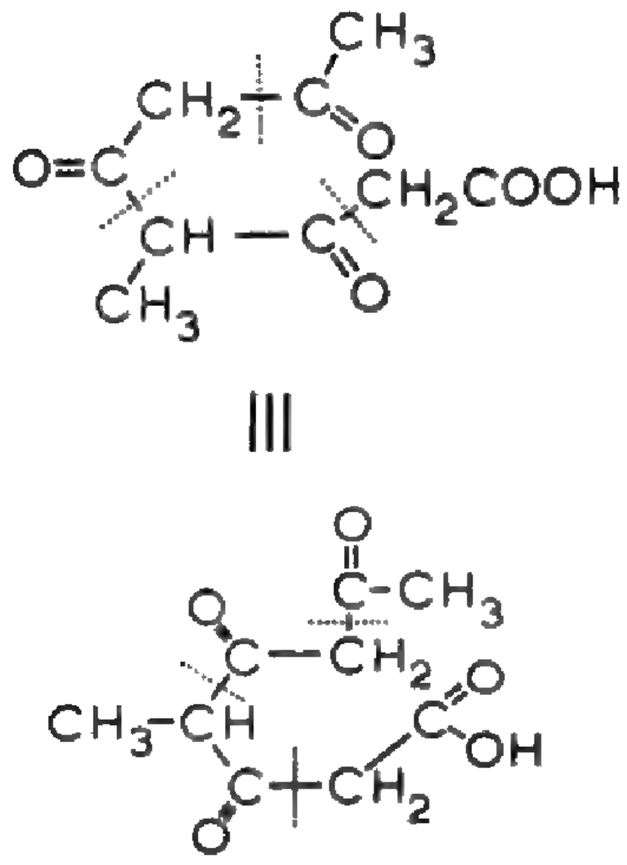


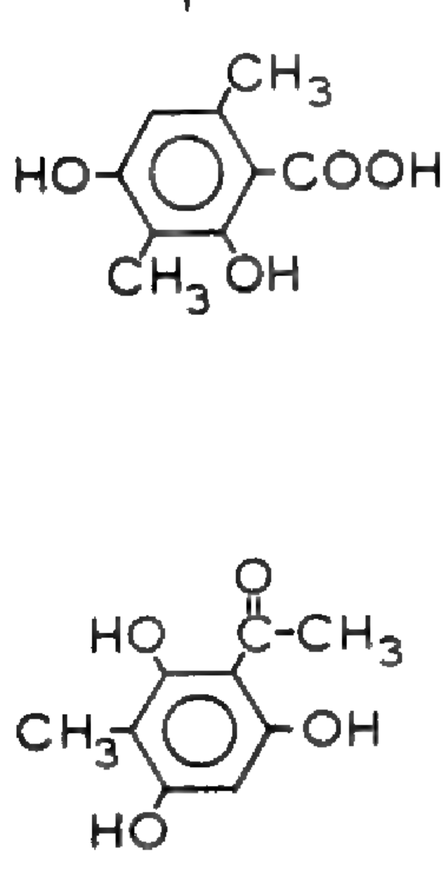
β-orcinol-type depside
(atranorin)





β-orcinol-type depsidone
(fumarprotocetraric acid)





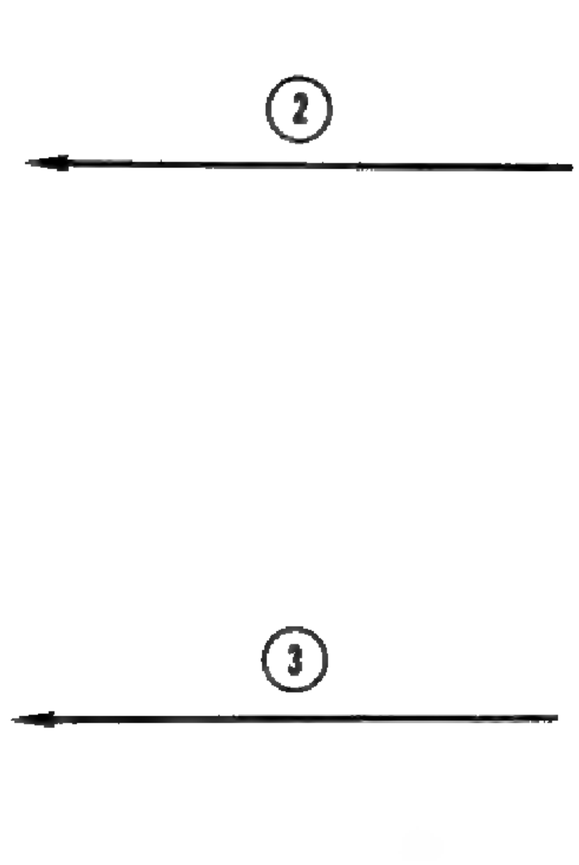


FIGURE 4. A comparison of the structures of orcinol- and β-orcinol-type compounds and two possible biosynthetic pathways (numbered "1" and "2") leading to β-orcinol units. The precursor in pathway "2" could cyclize by pathway "3" to the phenolic unit from which usnic acid is derived.

a discussion, see Whalley, 1963). Perhaps it is not just a coincidence that the same branched carbon chain, cyclizing by a different mechanism, would yield the phenolic ketone required for the synthesis of usnic acid (Figure 4, pathway "3"). Usnic acid and atranorin are by far the two most common lichen substances. Both are found mainly

in the upper cortex rather than in the medulla where most of the depsides and depsidones accumulate. The production of a depside or a depsidone in the medulla and either atranorin or usnic acid in the cortex is the most striking pattern observed in the histological distribution of chemical compounds in the macrolichens. Yet the chemical structures of atranorin and usnic acid are so distinct that the possibility of their synthesis from similar starting materials was not immediately obvious.[1]

The production of β-orcinol-type *versus* orcinol-type substances may have distinct taxonomic significance since many groups of lichens show a strong tendency toward the production of one type of compound or the other. In the genera studied here, the medullary constituents of *Cetrelia* are all orcinol-type depsides and depsidones while a β-orcinol depsidone occurs in *Platismatia*. Atranorin, a β-orcinol depside, is found in the upper cortex of all the species of both genera.

LENGTH AND OXIDATION STATE OF THE SIDE CHAIN IN ORCINOL-TYPE PHENOLIC ACIDS

Figure 3 shows how one acetate and three malonate units could condense to form orsellinic acid, a precursor of many lichen and fungal products. Starting with more than four units would give similar ring systems with a longer side chain. Since each malonate unit contributes two carbons to the final product, the side chain will increase in length in two-carbon steps. Side chains known in lichen substances are C_1, C_3, C_5, and C_7. Figure 5 shows the basic phenolic units of the orcinol-type compounds. In the *Cetrelia* compounds, side chains contain five or seven carbons except in ring B of imbricaric acid, which has a three-carbon substituent. In these species there is a tendency toward production of substances with longer side chains than are typical for lichens in general. The orsellinic acid ring, so common in the sub-

[1] After this section was written, three studies relating to the biosynthesis of atranorin and usnic acid appeared. Taguchi, Sankawa, and Shibata (1966) elegantly demonstrated that acetate-malonate-derived methylphloroglucinol self-condenses to give usnic acid and that the extra methyl group is indeed incorporated before the aromatic ring is formed. Yamazaki, Matsuo, and Shibata (1965) studied the labeling of lecanoric acid, atranorin, and chloroatranorin in *Parmelia tinctorum* fed with ^{14}C-labeled acetate and formate. They found incorporation of ^{14}C in all three substances when the lichen was fed with labeled acetate, but only in atranorin and chloroatranorin, which are the β-orcinol-type depsides, when the lichen was fed with labeled formate. The results indicate that the extra C_1 substituents are supplied by formate. In a second study, Yamazaki and Shibata (1966) showed that ^{3}H-labeled orsellinic acid and β-orcinolcarboxylic acid are incorporated exclusively into lecanoric acid and atranorin, respectively, proving that the extra C_1 substituent is added before aromatization during the biosynthesis of atranorin.

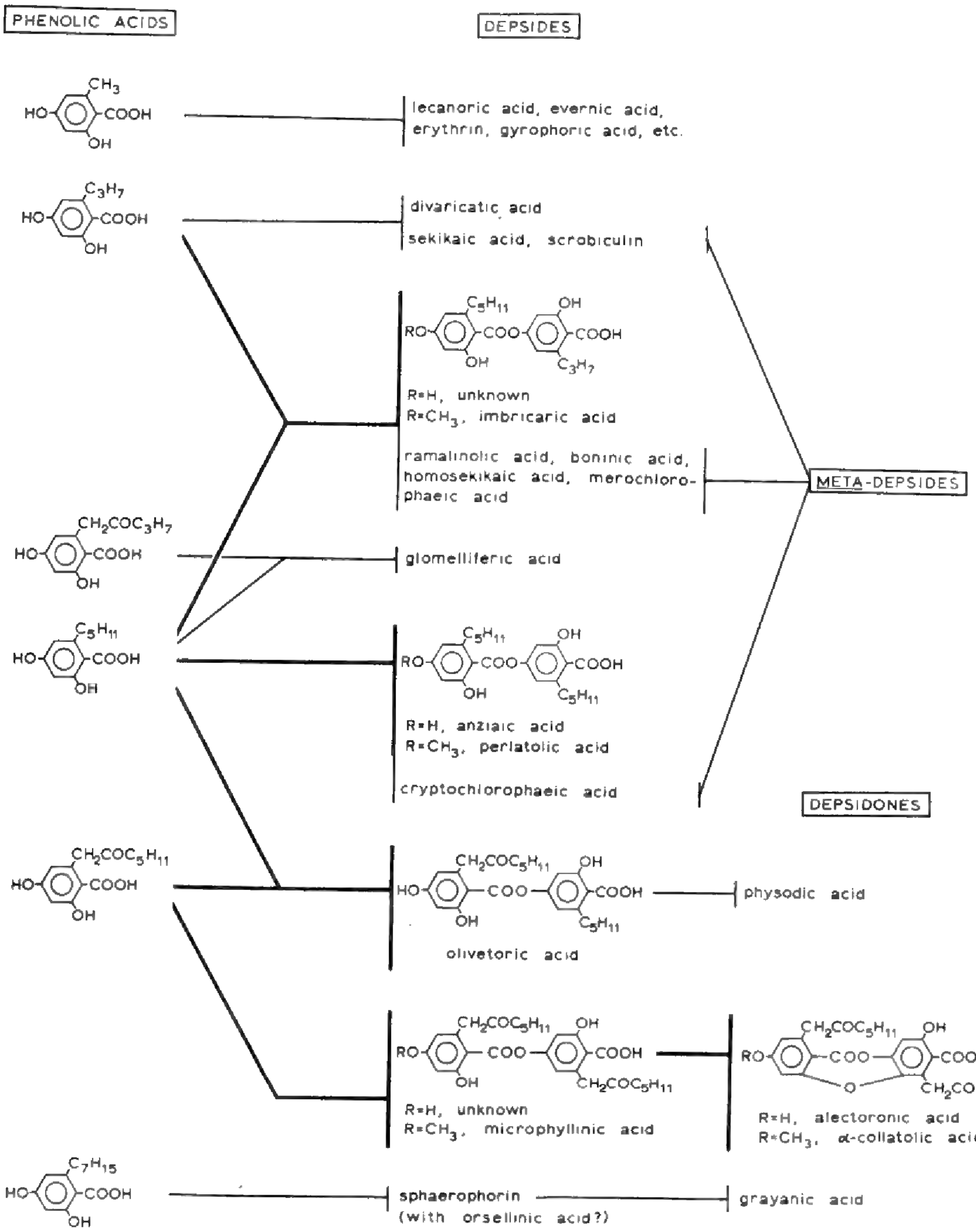


FIGURE 5. Chart showing the phenolic units (left column) incorporated in depsides (middle column) and depsidones (right column). The heavier lines lead to substances found in *Cetrelia* and the chemical structures of these compounds are given. The thinner lines lead to related substances known from other genera of lichens and are indicated for purposes of comparison. The phenolic units are arranged from top to bottom in order of increasing side chain length. Where two phenolic units have side chains of the same length, the less derived (the β-keto type) is given first. This arrangement shows that most of the medullary compounds in *Cetrelia* are both closely related to each other and also more highly derived within the framework of chemical variation shown by orcinol-type depsides and depsidones.

stances in many groups of lichens, is not involved in any known medullary constituents of *Cetrelia*.

Some orcinol-type phenolic rings in lichen substances retain a carbonyl group at the β-carbon of the alkyl side chain. The position of this carbonyl group corresponds to that of one of the original malonate carboxyls, and it seems probable that the β-keto groups result when there is no reduction at this position rather than by a new oxidation step. Lobaric acid and norlobaridone each have an α-keto group which probably forms by oxidation of a previously reduced side chain. Thus compounds with α-keto side chains may be more derived than compounds with fully reduced side chains, which in turn may require more steps for synthesis than a substance with a chain of equal length which retains a β-keto carbon.

In the orcinol-type depsides and depsidones of *Cetrelia*, the C_7 side chains retain a β-keto group while the C_3 and C_5 side chains are fully reduced (Figure 5). Except for the one C_3-substituted compound (imbricaric acid), biosynthesis of every phenolic unit in the *Cetrelia* compounds must involve reduction of two carbonyls, either to the $-C_5H_{11}$ group or to the $-CH_2COC_5H_{11}$ group. Oxidized C_3 alkyl groups are unknown in lichen substances, and a β-keto C_5 substituent is known only in glomelliferic acid.

Thus the biosynthesis of the KC+ compound microphyllinic acid may proceed through exactly the same steps required to synthesize perlatolic acid (KC−) except that the initial condensation leading to the phenolic rings in microphyllinic acid includes one extra malonate unit. In olivetoric acid, one ring is substituted as in perlatolic acid and the other as in microphyllinic acid.

DEPSIDES AND DEPSIDONES

For many years it was supposed that depsides were converted to depsidones by the loss of water from phenolic groups properly placed on each ring. There was, however, no known lichen depside with a structure suitable to give a known lichen depsidone by this route. It is now generally accepted that depsidones form from depsides by a loss of hydrogen in an oxidative-cyclization process (Figure 6) (Erdtman, 1962; Erdtman and Wachtmeister, 1957). A number of depside-depsidone pairs are known which show very similar ring substituents. In *Cetraria ciliaris* sens. lat. and in some individuals of *Pseudevernia furfuracea* (= *Parmelia furfuracea*), the depside-depsidone pair olivetoric acid and physodic acid occur together (C. F. Culberson 1964, 1965).

If the mechanism shown in Figure 6 is correct, then methylation of any phenolic hydroxyl or even the carboxylic acid group would disrupt

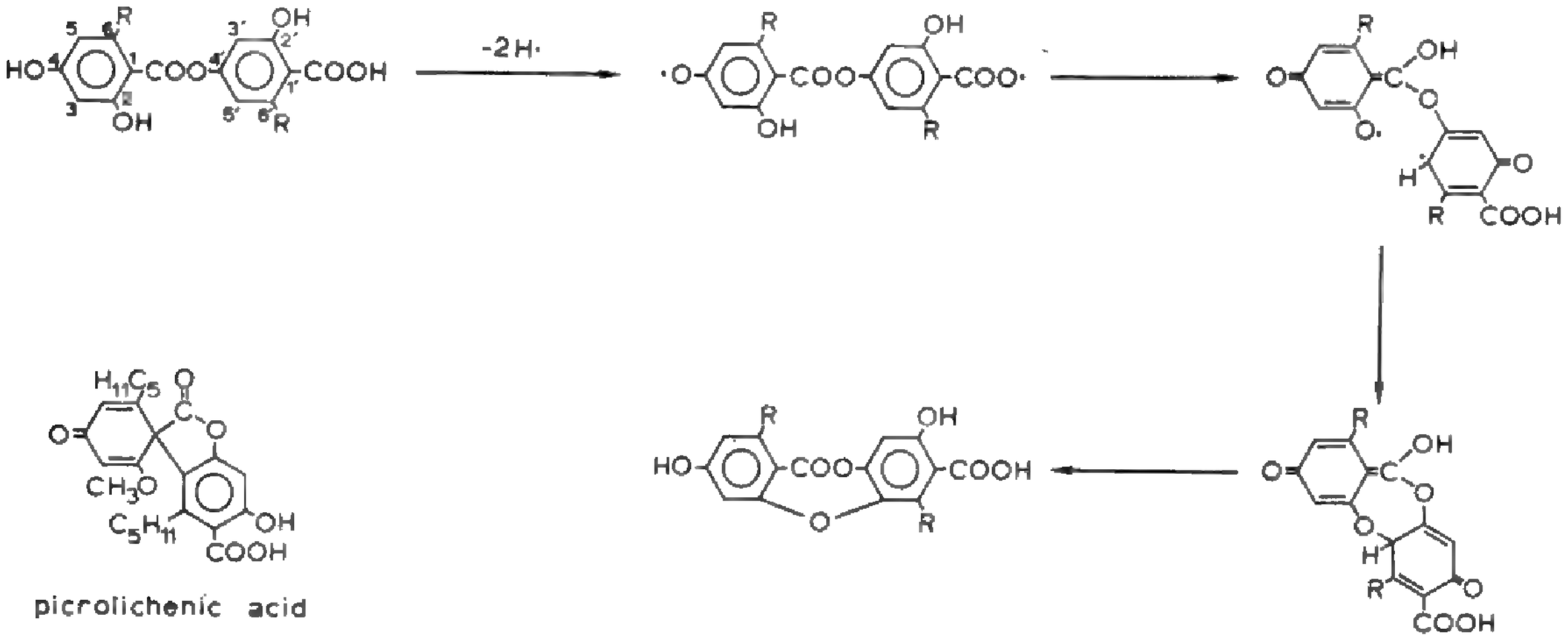


FIGURE 6. A possible biosynthetic route from depsides to depsidones. Picrolichenic acid is formed when oxidative coupling is blocked by 2-O-methylation. (See the text for fuller explanation.)

the formation of a depsidone from a depside. It has been pointed out (Erdtman and Wachtmeister, 1957) that methylation of the phenolic group *ortho* to the ester linkage can explain the formation of picrolichenic acid (Figure 6) by a mechanism similar to depsidone formation. But methylation at either the 4- or the 2′-hydroxyl may block cyclization altogether. Microphyllinic acid, which occurs in *Cetrelia*, is a depside closely related to alectoronic acid and α-collatolic acid, but it is methylated at the 4-hydroxyl. The related unmethylated depside is not yet known from lichens, but it would be the immediate precursor of the common lichen substance alectoronic acid. The latter substance could then be converted to α-collatolic acid by 4-O-methylation (Figure 5).

Blocking oxidative-cyclization reactions by methylation of hydroxyls that would pass through a quinoid structure during the cyclization is known in the biosynthesis of certain alkaloids where "it seems probable that methylation precedes and controls the direction of oxidative coupling. . ." (Scott, 1965).

O-METHYLATION

Methylation on oxygen is a very common and simple cause of chemical variation in lichen depsides and depsidones. All the phenolic groups in the molecule as well as the carboxylic acid group of ring B of orcinol-type depsides are subject to methylation, but methyl substitution at the 4-hydroxyl is most frequently observed. Examples among the *Cetrelia* compounds (Figure 5) are perlatolic acid, which is 4-O-methylanziaic acid, and α-collatolic acid, which is 4-O-methylalectoronic acid.

As yet there is no experimental evidence to indicate when methylation occurs, but the biosynthesis of picrolichenic acid requires 2-O-

methylation before oxidative cyclization. On the other hand, if 4-O-methylation or 2′-O-methylation can block depsidone formation as suggested above, then depsidones must be methylated at these positions after oxidative cyclization.

It seems that the order of methylation may vary and perhaps the taxonomic significance of substances which differ by methylation alone will also vary. In *Cetrelia*, for example, anziaic acid and perlatolic acid do not seem to occur together and the species in which they occur appear to be very distinct, while alectoronic acid and α-collatolic acid are always found together and seem to be more closely related biosynthetically.

RELATIONSHIP OF *CETRELIA* COMPOUNDS TO OTHER LICHEN SUBSTANCES

Figure 5 shows the orcinol depsides in *Cetrelia* and some closely related substances from other lichens. The chart is arranged to show, in a very general way, the relationships among these substances and the extreme uniformity of the structures involved. All seven medullary compounds in *Cetrelia* may be derived from three phenolic-acid units and six of the substances from only two such units. Reactions probably required in the biosynthesis of these compounds are (1) esterification of the phenolic units, (2) 4-O-methylation (in imbricaric acid, perlatolic acid, α-collatolic acid), and (3) oxidative cyclization to a depsidone (in alectoronic acid and α-collatolic acid). (See the caption of Figure 5 for additional explanation.)

The *Cetrelia* substances do not show some of the variations observed in other orcinol-type depsides and depsidones. O-Methylation occurs only at the 4-hydroxyl, for example, and more highly methylated substances, such as planaic acid (a methyl ether of perlatolic acid) and confluentic acid (a trimethyl ether of olivetoric acid), are not found in *Cetrelia*. Nor are *meta* depsides found, although many of the known *meta* depsides could be derived from the same phenolic acid units involved in the *Cetrelia* compounds. Perhaps some of the minor constituents not identified in the present study will represent modifications of chemical structure.

While the *Cetrelia* substances seem to be uniform, the synthesis of α-collatolic acid, a monomethyl ether depsidone, represents a certain degree of advancement over, say, the production of simple depsides such as lecanoric acid. The production of relatively advanced but highly uniform chemical substances would substantiate the concept of these species as evolved from ancestors which produced such complex compounds as alectoronic acid and α-collatolic acid. If this is true, the other substances found here might have resulted from a

retrogressive evolution in which reactions leading to alectoronic acid and α-collatolic acid became blocked or modified.

Considering the complete lack of direct evidence, other plausible theories to account for the production of these substances could be advanced, but the route suggested here is the simplest one in the light of present knowledge. This hypothesis would support the concept of the origin of *Cetrelia* from an *Amphigymnia*-type ancestor producing alectoronic acid and α-collatolic acid. Hale (1965) found that alectoronic acid (usually with α-collatolic acid) is indeed the most common medullary substance in *Parmelia* subgenus *Amphigymnia*. As in *Cetrelia*, all of these species also produce atranorin in the cortex, but unlike *Cetrelia* the other species of *Amphigymnia* Parmelias produce a wide variety of chemical substances including fatty acids, *meta* depsides, orsellinic acid-derived depsides, and β-orcinol depsidones. It is significant that the common cortex substance usnic acid is produced in *Parmelia* subgenus *Amphigymnia* but not in *Cetrelia*, and it is further noteworthy that usnic acid never occurs in those *Amphigymnia* Parmelias which produce alectoronic acid or olivetoric acid.

Methods for the Microchemical Identification of Lichen Substances in *Cetrelia* and *Platismatia*

The aim of this section is to give a complete description of the most reliable and convenient tests for determining the constituents of the species treated in this monograph. The usual microcrystal tests (Asahina, 1936–1940) and paper-chromatographic methods (Wachtmeister, 1959) have been used to identify the lichen substances in herbarium specimens in this study, although in the time since the research reported here was done thin-layer chromatography has become the major chromatographic technique in lichen microchemistry. The descriptions here are intended to give the taxonomist enough information for reliable, practical identifications of the nine substances involved in *Cetrelia* and *Platismatia* and are not meant as a complete treatment of all the microcrystal or chromatographic tests which might conceivably be used for these substances. The methods described are sufficient to distinguish these substances from each other as they occur in our genera, but alone they might not be sufficient to identify the same substances in all the other lichens for which additional constituents might introduce complications. In the research described here, many other tests were actually used. These studies were necessary to establish the data reported, but they are not required for routine identifications in specimens of *Cetrelia* and *Plastismatia* now that the major constituents are known.

SOLUTIONS

The following solutions are used in the microchemical procedures to be described:

1. GE solution. A mixture of three parts of acetic acid and one part of glycerin.
2. GAW solution. A mixture of equal volumes of ethyl alcohol, water, and glycerin.
3. ĠA*o*-T solution. A mixture of one part *o*-toluidine, two parts alcohol, and two parts glycerin. The solution should be discarded when it turns red. A nearly colorless solution can be prepared if the *o*-toluidine is first distilled from zinc powder.
4. 5 percent NaOH. A solution of 5 grams of sodium hydroxide in 95 ml. of water.
5. Ammonium hydroxide-saturated n-butanol. Concentrated ammonium hydroxide is added to n-butanol and the mixture is shaken thoroughly in a separatory funnel or bottle (the gas pressure frequently being released). Sufficient ammonium hydroxide is added so that, after shaking, two layers will separate. The upper layer and a smaller amount of the lower layer are placed in the chromatographic tank.
6. Pyridine-ethyl acetate-water. A mixture of one part pyridine, two parts ethyl acetate, and one part water.
7. Diazotized benzidine. Dissolve 1.7 grams of benzidine dihydrochloride in 250 ml. of water and add 3 ml. of concentrated hydrochloric acid. Prepare a separate solution of 25 grams of sodium nitrite in 250 ml. of water. Just before use, one part of the sodium nitrite solution is added, by drops, to one part of the benzidine solution.
8. Stable PD. A solution of 10 grams of sodium sulfite and 1 gram of *p*-phenylenediamine in 100 ml. of water to which is added 0.5 ml. or less of a wetting agent (such as "Photoflo").
9. 0.1 M Na_3PO_4. A solution of 3.8 grams of trisodium phosphate dodecahydrate in 100 ml. of water.
10. 1 N H_2SO_4. A solution prepared by adding 3 ml. of concentrated sulfuric acid to 97 ml. of water with stirring.

In addition to these solutions, acetone, benzene, ethyl alcohol, and ethyl ether, and the usual spot test reagents are used in the microcrystal and paper chromatographic procedures to be described.

MICROEXTRACTION

Thallus fragments equivalent to approximately one square centimeter are placed in a shell vial (1.2 by 3.5 cm.) and enough benzene is added to cover the sample. After about 5 minutes the benzene is decanted onto a microscope slide on a slide-warming tray (about 55°C). The extraction with benzene at room temperature is repeated twice more, and the solutions are evaporated on the same heated slide. Then the vial is placed on the warming tray and just enough acetone is added to cover the sample. The fragments are extracted for 5 to 10 minutes and the solution is then evaporated on another heated slide. This procedure is repeated twice more, as was done for the benzene extraction. The lichen sample is discarded, and then the two slides with the residues are ready for use.

MICROCRYSTAL TESTS

The microcrystal tests are performed on portions of the residues from the acetone and benzene extracts. Small amounts of residue are removed with a razor blade and transferred to another slide. The amount of solid residue needed for a test depends primarily upon (1) the solubility of the crystals in the test solution, (2) the volume of test solution used, and (3) the concentration of the substance in the residue being tested. Using a very small cover slip reduces the volume of test solution applied and consequently the amount of solid residue required for a crystal test. If the crystal test fails the first time, a second test with more (or sometimes less) of the residue often gives better results.

Solutions for the crystal tests described below are the GE, GAW, and GA*o*-T solutions and a 5-percent aqueous NaOH solution. A drop of the test solution is applied to a cover slip which is gently placed on the residue so that the liquid covers the solid. Tests with the GA*o*-T solution and with 5 percent NaOH usually do not require heat. Tests with the GE and GAW solutions depend upon a recrystallization process and the slides should be warmed, preferably over a microflame. Many of the substances treated here are more soluble in the GE solution than in the GAW solution, and usually less heat is needed for tests in the GE solution. The solutions should not be allowed to boil, and heating should be stopped at once if the solid seems to dissolve rapidly. Most preparations are now ready for microscopic examination. If crystals have not formed, the slides are reexamined later.

PAPER CHROMATOGRAPHY

Paper chromatograms are generally prepared on Whatman No. 1 paper although other types of paper (e.g., Whatman No. 3 MM and

Toyo Roshi No. 50) are equally satisfactory. The chromatograms are developed by the ascending method, which is simpler than the descending method and requires less elaborate equipment. Any chromatographic tank is satisfactory, but ideally it should be tall enough for development of the chromatograms to 15 to 20 cm. and still not so large that it becomes difficult to saturate the atmosphere in it with the developing solvent. A filter-paper lining around the inside of the tank helps to keep the atmosphere saturated.

The spots of the extracts are applied 1.5 cm. apart along a line 3 cm. from the bottom of the paper. A small amount of the residue on the slide is treated with a drop of acetone, and a portion of this solution is drawn by capillarity into a narrow glass tube with an inside diameter of about 1 mm. (thin-walled capillary tubing which has been pulled out in a flame to a point). The tip of the tube is then touched several times to a marked point on the starting line. With care, the spots can be kept 3 to 5 mm. in diameter, thereby producing better results with less material than larger spots would. The amount of substance needed for the chromatogram depends largely on how its constituents separate and the sensitivity of the spray reagent. The reagents used in the present study are extremely sensitive, and the spots are easily overloaded. The optimum quantity of material to be applied to a spot can be judged easily after a few trials.

Paper chromatograms of all substances described here except fumarprotocetraric acid are developed in ammonium hydroxide-saturated n-butanol. With this solvent there are two liquid layers. The upper layer is ammonium hydroxide-saturated n-butanol and the chromatogram should be adjusted so that it dips into only this layer. For paper chromatograms of fumarprotocetraric acid, the single-phase solvent pyridine-ethyl acetate-water (1:2:1) is used.

When the chromatogram has developed to a height of 15 to 20 cm., it is dried and then viewed with ultraviolet light. Both long- (366 mμ) and short-wave (254 mμ) lamps were used in the present study. The short-wave light was superior largely because it delivered much less visible light than the particular long-wave lamp available, and the fluorescent spots are more easily distinguished in darkness. The spots are encircled in pencil and labeled for color of fluorescence.

Chromatograms run in ammonium hydroxide-saturated n-butanol are sprayed with a freshly prepared diazotized benzidine solution, and after a few minutes the paper is washed with cold water and dried. Chromatograms of fumarprotocetraric acid developed in pyridine-ethyl acetate-water are sprayed with the stable PD solution. The chromatograms should be sprayed in a hood or in some way so that the mist of the reagents is not inhaled.

All paper chromatograms should be saved. Chromatograms sprayed with stable PD can be kept for some time in a large plastic envelope.

HYDROLYSIS OF DEPSIDES

The depsides imbricaric acid and perlatolic acid can be confirmed by chromatography of the hydrolyzed residues, and this procedure is also particularly useful in distinguishing olivetoric acid from anziaic acid. The methods described here are slightly modified from those suggested by Wachtmeister (1956) and have been presented in detail elsewhere for imbricaric acid and perlatolic acid (C. F. Culberson and W. L. Culberson, 1965).

A portion of the extract containing the unknown substance is removed from the residue slide with a razor blade and transferred to a vial. The amount required is usually about two to four times as much as is needed for a microcrystal test. The residue is covered with three or four drops of 0.1 M Na_3PO_4. The tube is kept stoppered at room temperature or very gently warmed for 15 to 24 hours. After this time most substances produce yellow, orange, pink, or red colors. A little ether is added, and after a few minutes the tube is closed and shaken sufficiently to mix the two layers. When the layers separate, the upper (ether) solution is drawn off carefully to avoid including any of the lower (aqueous) one. The ether solution is evaporated on a warmed slide and the extraction is repeated twice. This extract will usually contain phenolic substances and possibly excess starting material. Next, the aqueous layer is acidified with two drops of 1 N H_2SO_4 and extracted with ether as before, evaporating the ether extracts on a second slide. Both extracts are chromatographed in the ammonium hydroxide-saturated n-butanol solvent and the chromatogram is viewed with UV light and sprayed with diazotized benzidine.

Residues may also be hydrolyzed with concentrated sulfuric acid. The solid is placed in a vial and covered with two or three drops of the acid. After ten minutes at room temperature or (better) in a refrigerator, the tube is filled with crushed ice. When the ice melts the solution is extracted with ether three times as described above; the ether solutions are evaporated on a slide; and the aqueous layer is discarded. The residue is chromatographed as described above.

The appearance of the chromatograms from hydrolyzed extracts will vary with the degree of decarboxylation and other side reactions depending upon the particular conditions of the extraction, but the results from this simple test can be particularly valuable.

THIN-LAYER CHROMATOGRAPHY

After the completion of the microchemical studies for this monograph, the technique of thin-layer chromatography was developed

(Stahl, 1965) and has subsequently been applied successfully to the determination of many lichen substances. Thin-layer chromatography was employed briefly using samples of *Cetrelia* previously studied by the conventional microchemical methods, and in general good results were obtained. For some species, additional spots could be observed which were not found by paper chromatography, but these constituents, present in minute quantities, could not be identified. Table 4 gives the R_f values found for the eight substances known from *Cetrelia*. The chromatograms were run on air-dried silica gel-G plates developed with n-hexane-ethyl ether-formic acid and sprayed with 10 percent H_2SO_4. The plates were dried in an oven at 70°C and the color of the spots varied somewhat with the duration and conditions of drying. On the same chromatograms, extracts of *Platismatia lacunosa* containing fumarprotocetraric acid showed a black spot at the origin.

TABLE 4.—*R_f values in thin-layer chromatograms for compounds known in* Cetrelia. *The chromatograms were made on air-dried silica gel-G plates, developed with n-hexane-ethyl ether-formic acid to a height of 10 cm., sprayed with 10 percent H_2SO_4, and then dried at 70°C.*

Substance	R_f	Color After Spraying
Alectoronic acid	0.22	brown
Anziaic acid	0.50	yellow
Atranorin	0.73	yellow-brown
α-Collatolic acid	0.28	brown
Imbricaric acid	0.66	yellow
Microphyllinic acid	0.35	red-brown
Olivetoric acid	0.35	yellow-brown
Perlatolic acid	0.73	yellow

Identification of Specific Substances

ALECTORONIC ACID AND α-COLLATOLIC ACID

PLATE 1, FIGURES 1–3

The medulla of samples containing alectoronic acid or alectoronic acid and α-collatolic acid shows a strong KC+ reaction and a brilliant white fluorescence in UV light. Neither substance gives a color test with K, C, or PD. The microchemical tests used to identify these compounds in the present study have recently been described elsewhere (W. L. Culberson and C. F. Culberson, 1965).

Benzene at room temperature dissolves some alectoronic acid and α-collatolic acid. Since α-collatolic acid is slightly more soluble in this solvent than alectoronic acid is, small quantities of α-collatolic acid in the mixture can often be detected better in the benzene extract than would be possible using a single acetone extraction.

Plate 1, Figures 1–2, shows examples of the variable crystal form of alectoronic acid and α-collatolic acid cocrystallized from the GE solution. Crystal morphology in the GAW solution is also variable and a common crystal type is illustrated (Plate 1, Figure 3). The final identification of these substances must be made by chromatography. In ammonium hydroxide-saturated n-butanol, alectoronic acid shows a spot at R_f 0.24 which appears bluish in UV light and turns deep red with diazotized benzidine. On the same chromatogram, α-collatolic acid produces a long spot at about R_f 0.56 which shows a pale fluorescence in UV light and turns dark red with diazotized benzidine. The spot for atranorin runs between that for alectoronic acid and that for α-collatolic acid.

ANZIAIC ACID

Plate 1, figures 4–5

All *Cetreliae* showing a C+ medullary reaction contain either anziaic acid or olivetoric acid. Anziaic acid is less common. Like olivetoric acid, it shows no color reactions with K or PD. Anziaic acid is slightly more soluble in benzene than is olivetoric acid, which is only scarcely soluble. The benzene extract contains atranorin along with anziaic acid, and the subsequent acetone extract contains more anziaic acid, often accompanied by more atranorin.

Frequently no crystals of anziaic acid form in the GE solution because the compound is very soluble there, but when recrystallization does occur, there are clusters of small, curved needles (Plate 1, Figure 4). Anziaic acid recrystallizes more dependably from the GAW solution, but the curvature and size of the needles which form (Plate 1, Figure 5) are variable. Unlike olivetoric acid, anziaic acid does not produce very persisting crystals in the GA*o*-T solution. Colorless needles which may be present in a fresh GA*o*-T preparation soon dissolve.

Anziaic acid chromatographs well in ammonium hydroxide-saturated n-butanol giving a spot at R_f 0.67 which is blue in UV light and bright red with diazotized benzidine. While there may be a slight red coloration with diazotized benzidine just above the spot for anziaic acid, the chromatogram is distinguishable from the typical double spot produced by olivetoric acid near the same R_f value. Determination of anziaic acid can be confirmed by hydrolysis since chromatographic analysis then shows a single spot for olivetol-2-carboxylic acid near R_f 0.60.

ATRANORIN

PLATE 1, FIGURE 6; PLATE 2, FIGURES 7–10

A number of papers describe the microchemical identification of atranorin. This compound turns yellow with K and pale yellow with PD, although the latter reaction is rarely observed on the thallus. Atranorin is somewhat soluble in benzene at room temperature but is usually found in the subsequent acetone extract as well unless it is present in the thallus in only very small concentration. Colorless prisms in the GE solution (Plate 1, Figure 6) and yellow needles in the GA*o*-T solution (Plate 2, Figures 7–8) are used to identify this substance. The crystal test in GA*o*-T is very sensitive (C. F. Culberson, 1963), and it is usually successful even in the presence of other compounds. Large concentrations of alectoronic acid, α-collatolic acid, and especially microphyllinic acid, however, may inhibit the crystal formation of atranorin in the GA*o*-T solution and also sometimes may decrease the size or alter the appearance of the prisms in the GE solution. The shade of yellow of the crystals in the GA*o*-T solution is somewhat variable, perhaps due to the presence of chloroatranorin or other compounds in the samples. Two types of atranorin crystals in the GA*o*-T solution are shown (Plate 2, Figure 9). The smaller, finer, more sharply curved needles are also a somewhat deeper yellow color. Atranorin is sparingly soluble in alcohol and does not recrystallize from the GAW solution.

Chromatography in ammonium hydroxide-saturated n-butanol gives a good spot (R_f 0.53) which is yellow in the ammonia atmosphere of the developing tank, fluoresces yellow in UV light, and turns yellow with diazotized benzidine. In the pyridine-ethyl acetate-water developing solvent, atranorin travels with the solvent front ($R_f = 1$).

CAPERATIC ACID

PLATE 2, FIGURES 11–12; PLATE 3, FIGURES 13–18

The only fatty acid definitely proved to occur in the genera studied here is caperatic acid, but microcrystal tests are not a good method for identifying fatty acids, and it is certain that other constituents will be found when better techniques are perfected.

Caperatic acid shows no thallus spot tests. It is sparingly soluble in benzene at room temperature while protolichesterinic acid, another common fatty acid of lichens, dissolves readily. By extracting the thallus fragment first with benzene and then with acetone, these two fatty acids would be separated from each other. This solubility difference is fortunate since experiments with pure caperatic acid extracted from *Parmelia cryptochlorophaea* Hale (C. F. Culberson, 1965)

show that under certain conditions this compound produces crystals in the GE solution which are similar to those of protolichesterinic acid.

Normally, caperatic acid crystallizes from the GE solution as circular or cloud-shaped clumps appearing somewhat similar to drops of oil (Plate 3, Figures 13–14). These crystals are very distinctive and easily recognizable. But many GE preparations show plate-like crystals, singly or in radiating clusters (Plate 3, Figures 15–16), similar to those typical of protolichesterinic acid. Sometimes plate-like crystals seem to emerge from the circular ones (Plate 3, Figures 17–18). At first this gives the impression of a mixture of protolichesterinic acid and caperatic acid. But, since the lichen fragment was extracted first with benzene and this extract showed no protolichesterinic acid, the presence of protolichesterinic acid in the second residue is not likely.

Chemical transformation of caperatic acid into protolichesterinic acid under the influence of acetic acid in the GE solution is extremely unlikely. A careful comparison of the crystal shapes indicates two possible explanations: (1) either caperatic acid has two crystal forms or (2) caperatic acid here is sometimes converted to some substance other than protolichesterinic acid. The most obvious reaction which might occur in the GE solution is the hydrolysis of the methyl ester of caperatic acid, giving norcaperatic acid. A sample of pure norcaperatic acid showed crystals (Plate 4, Figure 19) in the GE solution that were very similar to, but probably not identical with, the cloud-type crystals of caperatic acid. The crystals of norcaperatic acid in the GAW solution (Plate 4, Figure 20) are indistinguishable from those of caperatic acid.

Crystals of caperatic acid in GAW solution are very small circular plates usually clustered into large radiating aggregates (Plate 2, Figure 12). In some preparations there are curly crystals, especially at the center of the aggregates of caperatic acid (Plate 2, Figure 11), perhaps of an unidentified fatty acid.

Caperatic acid shows small, fuzzy, colorless balls in the GA*o*-T solution, and it distorts the yellow crystals produced by atranorin when the latter substance is also present (Plate 2, Figure 10).

When samples containing caperatic acid are chromatographed in ammonium hydroxide-saturated n-butanol, a weakly fluorescing, trailing spot may be found near R_f 0.75. When the chromatogram is sprayed with diazotized benzidine to reveal atranorin or other compounds, the spot for caperatic acid turns very pale yellow and, while the chromatogram is still wet, is barely visible. This is not, of course, a reliable method for identifying caperatic acid.

FUMARPROTOCETRARIC ACID

In this study one species, *Plastismatia lacunosa*, gave a positive test with PD and contained fumarprotocetraric acid. This substance is not

removed from the thallus by extraction with benzene at room temperature. Fumarprotocetraric acid dissolves in warm acetone but in this species it is accompanied by atranorin and usually also caperatic acid. From residues also containing caperatic acid, crystals of the *o*-toluidine derivative of fumarprotocetraric acid are not readily identifiable in the GA*o*-T solution, and all determinations of this substance were made by chromatography.

Paper chromatograms developed with ammonium hydroxide-saturated n-butanol show fumarprotocetraric acid as a dense streak near the origin. The spot turns dark red with diazotized benzidine and differs little in appearance from that of several other PD+ depsidones. Extracts from specimens showing such a spot were rechromatographed in pyridine-ethyl acetate-water (1:2:1). With this solvent, fumarprotocetraric acid shows a distinctive spot (R_f 0.39) which quenches UV light and turns yellow after spraying with the stable PD reagent.

IMBRICARIC ACID

PLATE 4, FIGURES 21–23

The microchemical methods used to identify imbricaric acid are described in detail elsewhere (C. F. Culberson and W. L. Culberson, 1966). A pure sample of this substance extracted from *Cetrelia sinensis* was used to check the microchemical tests used on crude extracts from thallus fragments. Imbricaric acid is negative with K, C, KC, and PD, but the KC+ reaction of the thallus of many samples containing imbricaric acid requires that the latter substance be distinguished from both KC+ and KC− compounds—in this study perlatolic acid, alectoronic acid, α-collatolic acid, and microphyllinic acid.

Imbricaric acid is somewhat soluble in benzene at room temperature. The subsequent acetone extract is often gummy and less satisfactory for the microcrystal tests. The large needles formed in the GE solution (Plate 4, Figure 21) show oblique extinction (ϕ=45°) in polarized light and in this respect differ from those of all other substances encountered here. The needles in the GAW solution (Plate 4, Figure 22) also show oblique extinction (ϕ=45°). In the GA*o*-T solution, imbricaric acid forms colorless needles (Plate 4, Figure 23), probably its *o*-toluidine salt. In the crude extracts where atranorin is also present, fuzzy yellow crystals form (Plate 4, Figure 24). These crystals may result from cocrystallization since very similar crystals were observed when a mixture of pure imbricaric acid and pure atranorin was treated with the GA*o*-T solution.

By chromatography in ammonium hydroxide-saturated n-butanol, imbricaric acid undergoes slow hydrolysis giving a spot at R_f 0.78,

blue-white in UV light and orange-red with diazotized benzidine, which trails down from the spot to about R_f 0.38 to 0.43 due to the degradation product divaric acid. Imbricaric acid can be definitely distinguished from perlatolic acid by hydrolysis with acid or base and by observing the strong spot at R_f 0.38 for divaric acid. In most cases, however, the observation of crystals with oblique extinction in the GE and GAW solutions and chromatography of the unhydrolyzed material are sufficient to identify imbricaric acid.

MICROPHYLLINIC ACID

PLATE 5, FIGURES 25–27

Microphyllinic acid is negative with K, C, and PD but gives a strong red coloration with KC. In at least one report in the literature, microphyllinic acid was mistaken for alectoronic acid because both substances give a positive KC test and needles in the GE solution. But microphyllinic acid can be definitely identified by microcrystal tests and chromatography.

Some microphyllinic acid is removed from the thallus fragment by extraction with benzene at room temperature. Some atranorin is also extracted then. The subsequent acetone extract contains less microphyllinic acid and is often a dark gum that is difficult to work. The microcrystal tests usually give best results with the benzene extract. In the GE solution, straight radiating needles form (Plate 5, Figure 25) with an extinction angle of zero. Atranorin often crystallizes in the same preparation, although the microcrystal test for atranorin in the GA*o*-T solution is inhibited by microphyllinic acid. In the GAW solution, microphyllinic acid recrystallizes as long, fine, sparsely clustered needles with an extinction angle of zero (Plate 5, Figure 26). These crystals are most similar to those of perlatolic acid but do not resemble those of alectoronic acid. The most rapid method for distinguishing microphyllinic acid from the other KC+ substances in *Cetrelia* is by the crystals of the sodium salt (Plate 5, Figure 27) which precipitate from 5 percent aqueous sodium hydroxide.

Microphyllinic acid hydrolyzes completely during chromatography in ammonium hydroxide-saturated n-butanol, and two characteristic spots are observed. The upper one, (R_f 0.93), which shows a bright blue-white fluorescence in UV light and turns orange with diazotized benzidine, is due to the ring A fragment (Figure 5). The lower spot (R_f 0.49), which interferes with the chromatographic determination of atranorin, appears blue in UV light, turns dark red with diazotized benzidine, and is due to the ring B fragment. The same spots are observed after base hydrolysis.

OLIVETORIC ACID

PLATE 5, FIGURES 28–30; PLATE 6, FIGURE 31

Samples showing a positive thallus reaction with C may contain either anziaic acid or olivetoric acid. Olivetoric acid gives no coloration with K or PD, but turns red with C, and the color is still more intense with KC. Olivetoric acid is reported to give a green color with aqueous $Ba(OH)_2$ (Asahina, 1936) while anziaic acid does not give such coloration, but this reaction was not used in the present study. Olivetoric acid is only slightly soluble in benzene and less soluble in it than anziaic acid is. The benzene extract of thallus fragments with olivetoric acid and atranorin encountered in this study is usually a small, colorless crust which contains only a trace of olivetoric acid. The subsequent acetone extract contains more atranorin and abundant olivetoric acid.

In the GE solution, olivetoric acid is quite soluble and it crystallizes slowly as small, fine, curved needles forming a dense mat (Plate 5, Figure 28). Olivetoric acid is less soluble in the GAW solution, and it usually produces beautiful, curved needles (Plate 5, Figure 29), which are larger and thicker than those in the GE solution. The crystals of anziaic acid in the GE and GAW solutions (Plate 1, Figures 4–5) are sufficiently similar to those of olivetoric acid that tests using these crystallizing reagents may require confirmation. Olivetoric acid also produces crystals in the GA*o*-T solution without heating. These clusters of straight, colorless needles or needle plates (Plate 5, Figure 30; Plate 6, Figure 31) form rapidly and are usually mixed with the yellow crystals formed by atranorin. Although anziaic acid may show small colorless needles under the same conditions, these soon dissolve.

Olivetoric acid hydrolyzes during chromatography in ammonium hydroxide-saturated n-butanol producing a double spot—one center (R_f 0.73) turns dark bluish-red with diazotized benzidine and the other (R_f 0.60) turns dark red with the same spray. These spots correspond closely to those produced by base hydrolysis which gives a spot for olivetol-2-carboxylic acid that is blue in UV light and turns dark red with diazotized benzidine (R_f 0.59) and a second spot, from ring A, that is blue in UV light and dark bluish-red with diazotized benzidine (R_f 0.76). Anziaic acid also gives olivetol-2-carboxylic acid by hydrolysis but not the second spot at R_f 0.76.

PERLATOLIC ACID

PLATE 6, FIGURES 32–34

Perlatolic acid gives no color reactions with the usual reagents, but some specimens containing this substance show a positive reaction

with KC due to the presence of a still unidentified compound. This situation is also encountered with samples containing imbricaric acid. Because of the spurious KC+ reaction observed with perlatolic and imbricaric acid-containing samples, the microchemical tests must distinguish these substances from each other and from the known KC+ substances occurring in *Cetrelia*.

Extraction of the thallus fragment with benzene at room temperature removes a portion of the perlatolic acid along with atranorin. The benzene extract is usually cleaner and more easily crystallized with the microcrystal solutions than is the subsequent gummy acetone extract.

When either extract is treated with the GE solution, perlatolic acid recrystallizes as clumps of needles (Plate 6, Figure 32) with straight extinction. Atranorin is usually observed in the same slide. In the GAW solution, perlatolic acid forms needles (Plate 6, Figure 33) which are usually shorter than those of imbricaric acid and their angle of extinction is zero. Many residues containing perlatolic acid show large colorless crystals (Plate 6, Figure 34) in the GA*o*-T solution when a test is made for atranorin. These crystals are very different from those of imbricaric acid in the same solution, but they have not been observed regularly enough to provide a good test for perlatolic acid.

Perlatolic acid chromatographs in ammonium hydroxide-saturated n-butanol with an R_f of about 0.83 which is slightly higher than the R_f value for imbricaric acid. When the developing solvent is fresh, perlatolic acid hydrolyzes slightly and trails to an R_f of about 0.59 due to the formation of olivetol carboxylic acid. The spot for perlatolic acid appears blue-white in UV light and turns orange-red with diazotized benzidine. Chromatographic confirmation of the presence of perlatolic acid is obtained by acid or base hydrolysis and chromatography of the products. The spot for olivetol carboxylic acid is at R_f 0.59 as compared to that for divaric acid at R_f 0.38, which would be found by hydrolysis of imbricaric acid. This procedure has been described in detail (C. F. Culberson and W. L. Culberson, 1966).

AN UNIDENTIFIED SUBSTANCE

Plate 6, figures 35–36

An unidentified substance in several species of *Cetrelia* gives yellow crystal clusters (Plate 6, Figure 35) in the GE solution. Many of the same specimens showed fine yellowish-tan needles (Plate 6, Figure 36) in the GA*o*-T solution, and it is possible that the crystals in these two solutions are caused by the same compound. The yellow crystals in the GE solution usually form near the edge of the slide, and the solution in the center of the preparation does not appear yellow. This sug-

gests that the unidentified substance might not be a yellow pigment in the lichen but rather a colorless substance which turns yellow and deposits crystals in the GE solution where it is exposed to the air.

Chemical Criteria in the Taxonomy of *Cetrelia* and *Platismatia*

In the previous discussion of the generic traits of *Cetrelia* and *Platismatia*, the high level of chemical uniformity within each genus was pointed out, an internal homogeneity all the more notable considering the great magnitude of the chemical difference between the two genera (Table 2). Chemistry here offers a striking correlation with the other characteristics that define the genera. The use of chemistry in the study of *Cetrelia* and *Platismatia* has considerable theoretical interest for taxonomy because it shows (1) the value of chemistry in an instance where it becomes a major characteristic defining genera, (2) the usefulness at the species level of chemical variations that are highly correlated with morphological variations in a genus which has undergone evolutionary diversification in both chemistry and morphology (*Cetrelia*), and (3) an example of a chemically conservative genus (*Platismatia*).

The involvement of chemistry in addition to morphology in the formulation of taxonomic judgments in lichenology has had a limited but nonetheless distinguished history, some of the most refined examples of its use being the elegant taxonomic systems constructed by Yasuhiko Asahina in Japan and by the late Alexander Evans in this country. Although today an increasing number of biochemists are becoming interested in the unique natural products of the lichens, lichen taxonomists by and large continue to ignore chemical variation. The major objection that most lichenologists raise to chemical considerations in lichenology is that chemistry, especially at the species level, is not used in most other groups of plants and that consequently it should not be used in lichenology either. The slight taxonomic usefulness of corolla pigmentation in the flowering plants is regularly pointed to as proof of the inconsequential significance of chemical variation as an indication of the natural relationships of plants at the species level. In rejecting chemistry from taxonomic considerations, Almborn (1965) probably summed up most present-day lichenologists' views when he wrote: "It is essential that lichen taxonomy be founded on firm principles not deviating too much from those generally accepted in other plant groups."

While Almborn's view may appear to reflect the commendable caution that characterizes responsible scientific judgment, most taxonomists recognize that the taxonomic characters valuable in one group of plants may be of absolutely no value whatever in another. In speaking

of vascular plants, Cronquist (1964) remarked: "We have found, to our sorrow, that individual morphologic characters do not have a fixed, inherent taxonomic importance wherever they occur. Instead, they are only as important as they prove to be, in any individual instance, in marking groups that have been perceived on the basis of all the available evidence." This observation is no less true for the cryptogamic plants than for the vascular plants, and it is no less true for chemical characters than for morphologic characters. The best taxonomy is always eclectic. A blind rejection of a whole category of information—in this case chemical information—is as extreme and as philosophically unsound as the diametrically opposed view would be—namely, to insist upon reflecting in the taxonomic system every minute variation that a diligent chemist could find. In the actual practice of classification, the taxonomist needs considerably more latitude and freedom than either of these extreme positions would permit since the different types of chemical variation to be found in the lichens do not all seem to be equally important.

In order to explain how the chemical information found in the present study was actually applied to the formulation of the taxonomic judgments, it is necessary to recall what sort of chemical data were actually found—although there is nothing unique about the chemical information here. The nature of the chemical variation in *Cetrelia* and *Platismatia* is essentially like that found in all the rest of the macrolichens. The chemistry of the species of these genera can be characterized as the production of two histological categories of substances, the cortex constituent and the medullary constituent (or constituents).

Individuals of *Cetrelia* and *Platismatia* all produce atranorin as the upper-cortex constituent. No other lichen substance is produced in this tissue and apparently every individual of every species produces this constituent. The only other common upper-cortex substance, usnic acid, a very widespread constituent in *Parmelia* for example, is never produced in the two new genera. Since it shows no variation, upper-cortex chemistry in *Cetrelia* and *Platismatia* is of no taxonomic value.

The chemistry of the medulla is more variable, at least in *Cetrelia;* the individual produces one substance (or occasionally two), and the production of a given substance or of a given pair of substances precludes the production of other medullary compounds. If morphologically uniform or highly similar specimens show any qualitative variation in medullary chemistry, it is a variation of the typical replacement type in which one compound is substituted for another, usually with the chemically different populations showing different geographic ranges—for example, *Cetrelia japonica* with microphyllinic

acid in Japan and *C. sinensis* with imbricaric acid in Formosa and China.

In interpreting chemical data in lichen species, one is faced with two questions: (1) To what extent are the data on the nonoccurrence of given substances in specimens and in species really due to true absence and to what extent are they due merely to the failure of technique to reveal their presence? (2) What is the biological significance (and consequent taxonomic significance) of the chemical variations that are found?

The pattern of chemical variation in which every specimen produces one medullary compound (or occasionally one pair of compounds) and in which morphologically similar plants exist in one or several of "chemical races" is so well known that it is now clear that it is the major type of chemical variation in all the lichens. In the present study every species matches this chemical pattern in that every one has at least one distinct and constant medullary constituent. There are no specimens without medullary compounds. In the present study the constant medullary compounds are given high taxonomic significance. Morphologically similar or identical populations with different but constant medullary constituents are considered distinct species. (*Cetrelia collata* with imbricaric acid is considered distinct from *C. nuda* with α-collatolic and alectoronic acids.) The constant constituents of the species are listed in Table 2.

In addition to the constant constituent medullary compound, some populations show an additional substance (or additional substances) in some specimens but not in others. For example *Platismatia erosa*, *P. interrupta*, *P. formosana*, and *P. regenerans* all produce caperatic acid as the constant medullary constituent. In addition, in some individuals of all these species, an unidentified substance could be demonstrated. We do not know whether this substance occurred in all the specimens and was not detected because of the limitations of our chemical techniques or whether the compound is merely present in only part of the populations. Since it occurs in addition to another substance (caperatic acid) that is invariably present and since its real distribution is unknown, this and the few other "accessory" substances found have not been considered in the delimitation of species. Likewise, in *Cetrelia cetrarioides* we are not sure whether some specimens contain both perlatolic and imbricaric acids although it is certain that most specimens contain only one substance or the other. Therefore, in this instance we have not used chemistry in the taxonomy because we feel that the chemical variation in this widespread species is still too inadequately explained.

The above examples demonstrate how the apparent absence of chemical constituents in individuals and in species has been evaluated.

The second problem, interpreting for taxonomic purposes the level of biological significance of chemical variation, is far more difficult. Since little has been definitively proved concerning the biosynthesis of the substances involved, we cannot estimate how different biologically the chemical races of morphologically similar lichens really are. Five main categories of evidence, however, lead to the inevitable conclusion that in morphologically similar or identical populations the largest chemical variations (those based on the constant chemical components) reflect major genetic differences; namely: (1) the orderly, nonrandom replacement series that the major medullary compounds regularly display; (2) the fact that chemically different populations usually show different geographic distributions; (3) the observation, noted repeatedly in many genera, that where geographic ranges overlap and where chemically different populations become sympatric—and where consequently chemically different plants may even grow side by side—no chemically intermediate individuals are found; (4) the fact that in localities where the chemical races are sympatric and where some chemically different plants do exist side by side, the chemical races as a whole select different habitats (W. L. Culberson and C. F. Culberson, 1967); and (5) the lack of any indication whatever that environment has anything to do with the qualitative presence of the major medullary constituents.

For a few lichen substances, there is some biosynthetic information which helps in taxonomic evaluations. For example, it is believed that stictic acid is derived from norstictic acid by a simple, one-step methylation reaction. In a recent study of the *Ramalina siliquosa* group (W. L. Culberson, 1967), no taxonomic importance was attached to the demonstration of norstictic acid in some of the stictic acid-producing individuals because norstictic acid is the biochemically expected precursor of stictic acid. Unfortunately, much of our knowledge of the biosynthesis of the substances produced in the genus *Cetrelia* is less precise, but it should be pointed out that in the present study we have not involved in the defining of species limits any pairs of substances believed to have such an intimate biosynthetic relationship as that of norstictic and stictic acids. It is precisely in the area of interpreting the biological significance of chemical variation that the lichenologist of the future, with a more precise knowledge of the chemical relationships of the compounds, will hopefully be able to distinguish significant from inconsequential chemical differences just as we hope today to distinguish significant from inconsequential morphological differences.

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Taxonomic Treatment

Cetrelia Culb. et Culb., gen. nov.

Thallus (5–)7–24(–26) cm. latus; laciniae 0.5–2.0(–2.5) cm. latae. Superficies superior pallide cinerea, albida, vel apud exemplaria vetera herbarii pallide citrella, pseudocyphellata, isidiata vel sorediata. Superficies inferior picea, rhizinata, saepe punctata. Cortex superior 15–30(–34)μ crassus, prosoplectenchymatosus; medulla 85–230(–264)μ crassa, alba; cortex inferior (10–)12–25(–31)μ crassus. Apothecia (0.1–)0.5–2.0(–4.2) cm. lata, submarginalia, vulgo perforata; hymenium (53–)62–110(–124)μ crassum, asci IKI+ caerulescentes; strata subhymenialia (35–)40–78(–84)μ, IKI−, stratum conspicuum algarum fere tegentia. Sporae 8-nae, ellipsoideae, 11–22(–25)$\times$6–12μ. Pycnidia marginalia; conidia 1–1.5$\times$(3–)4–6μ, recta, extremis nonnihil inflatis. Typus generis *C. cetrarioides* est.

Thallus (5–)7–24(–26) cm. broad; lobes 0.5–2.0(–2.5) cm. broad. Upper surface ashy white or tan, pseudocyphellate, isidiate or sorediate. Lower surface black, rhizinate, punctate in some species. Upper cortex 15–30(–34)μ thick, prosoplectenchymatous; medulla 85–230 (–264)μ, white; lower cortex (10)12–25(–31)μ thick. Apothecia (0.1–) 0.5–2.0(–4.2) cm. broad, submarginal, usually perforate; hymenium (53–)62–110(–124)μ, the asci IKI+ blue; subhymenial layers (35–) 40–78(–84)μ, IKI−, usually underlain by a conspicuous layer of algae. Spores 8, ellipsoid, 11–22(–25)$\times$6–12μ. Pycnidia marginal; conidia 1–1.5$\times$(3–)4–6μ, rod-shaped, the ends slightly inflated.

Constituents: atranorin and alectoronic, anziaic, α-collatolic, imbricaric, microphyllinic, olivetoric, or perlatolic acids.

None of the species of the *Parmelia cetrarioides* group, recognized here as the genus *Cetrelia*, is the type of a validly described genus which could be used for them. Although *Cetraria sanguinea* Schaer., a member of the new genus, was included along with a *Parmelia* in the genus *Aspidelia* Stirt., that generic name is invalid (W. L. Culberson,

1966a). The name *Cetrelia* is a fanciful concoction from *Cetraria* and *Parmelia*, the genera in which most of the species had previously been placed.

Artificial Key to the Species of *Cetrelia*

1. Thallus sorediate or isidiate or both.
   2. Thallus sorediate, primarily along the margins of the lobes, not isidiate.
      3. Medulla C+ pink or pinkish-orange, olivetoric acid present; widely distributed . . . . . **11. C. olivetorum**
      3. Medulla C−, olivetoric acid absent; widely distributed.
         4. Medulla KC− or KC+ dirty pinkish, alectoronic acid and α-collatolic acids absent; widely distributed, common in Europe but rare in North America.
            5. Medulla usually KC−, perlatolic acid present. **3. C. cetrarioides** sens. str.
            5. Medulla usually KC+ dirty pinkish or rarely KC−, imbricaric acid present . . . . . **3. C. cetrarioides** sens. lat.
         4. Medulla KC+ bright pink or red, alectoronic and α-collatolic acids present; widely distributed, common locally in eastern North America but rare in Europe . . . . . **4. C. chicitae**
   2. Thallus isidiate, not sorediate.
      6. Isidia accompanied by conspicuous dorsiventral lobulae in tufts on the thallus surface or as a fringe along the margins of the thallus lobes . . **9**
      6. Isidiate plants without dorsiventral lobulae.
         7. Medulla C+ red, anziaic acid present; isidia often poorly developed; Formosa and Japan . . . . . **8. C. isidiata**
         7. Medulla C−, KC+ pink or red, alectoronic and α-collatolic acids present; isidia well developed and not at all sorediose through most of the range but granular, poorly developed and sorediose in the southern part (Philippines); Asia . . . . . **2. C. braunsiana**
1. Thallus neither sorediate nor isidiate.
   8. Thallus with dorsiventral lobulae in tufts or clusters on the upper surface or as a fringe along the margins of the lobes.
      9. Medulla C− ; lobulae well developed and abundant.
         10. Microphyllinic acid present; Japan and southeastern Asia. **9. C. japonica**
         10. Imbricaric acid present; China and Formosa . . **14. C. sinensis**
      9. Medulla C+ pink or red; lobulae well developed or poorly developed, infrequent, granular, and isidioid.
         11. Olivetoric acid present; Japan, Formosa, China, and the Himalayas. **12. C. pseudolivetorum**
         11. Anziaic acid present; mountains of southern and southeastern Asia and Japan . . . . . **13. C. sanguinea**
   8. Thallus without lobulae.
      12. Pseudocyphellae very small, rarely reaching 1 mm. long, simple and punctiform (Plate 12, Figure 52).
         13. Medulla C+ pink or red.
            14. Olivetoric acid present; mountains of southwestern China. **6. C. davidiana**
            14. Anziaic acid present; mountains of southern and southeastern Asia and Japan . . . . . **13. C. sanguinea** (some forms)
         13. Medulla C− ; perlatolic or imbricaric acid present.

15. Lobes relatively thick and uniformly colored; pycnidia conspicuously distributed along margins of the lobes; on trees, southwestern China. **7. C. delavayana**

15. Lobes relatively thin, the margins darker than the center; pycnidia unknown; on tundra soil in Alaska . . . . . **1. C. alaskana**

12. Pseudocyphellae very large, some more than 1 mm. long, compound and irregular (Plate 12, Figure 53).

16. Medulla KC+ pink, alectoronic and α-collatolic acid present; Japan, Formosa, and southwestern China . . . . . **10. C. nuda**

16. Medulla KC−, imbricaric acid present; southwestern China and Nepal. **5. C. collata**

1. Cetrelia alaskana (Culb. & Culb.) Culb. & Culb., comb. nov. PLATE 14

Cetraria alaskana Culb. & Culb., Bryologist 69:200. 1966. Type: U.S.A., Alaska, Cape Sabine, *Thomson, Lich. Arct.* 13 (DUKE, holotype; COLO, LD, MSC, WIS, WIS-Herb. Thomson, isotypes).

Thallus medium, 5–7 cm. broad, pale, yellowish-tan, or brownish, often mottled with black, the margins distinctly brown. Lobes 1–1.5 cm. broad, smooth, not pruinose, esorediate, pseudocyphellate, the pores minute. Lower surface jet-black throughout or the margins chestnut brown, smooth, not punctate, rhizines few, often very short and papilliform. Upper cortex 16–29μ thick; medulla 86–135μ thick; lower cortex 16–23μ thick. Apothecia and pycnidia unknown.

MEDULLARY REACTIONS.—K−, C−, KC− or KC+ pale pink, PD−.

CONSTITUENTS.—Imbricaric acid and atranorin.

DISTRIBUTION (Map, Figure 10).—The west coast of Alaska on the Bering Sea and Arctic Ocean; in the tundra.

Cetrelia alaskana is a conspicuous, large-lobed lichen inhabiting plant debris in the Alaskan tundra. It has doubtless been collected more frequently than the present records indicate and has consistently been mistaken for other species. The fact that it may be locally abundant is clearly shown by the fact that at Cape Sabine, the type locality, Thomson collected enough of the species to issue in his exsiccat series, *Lichenes Arctici*.

Cetrelia alaskana resembles *C. cetrarioides* more than it does any other species. Both have characteristic, minute, easily overlooked pseudocyphellae in the upper cortex. *Cetrelia alaskana*, however, can easily be distinguished from *C. cetrarioides* by its lack of soredia.

Cetrelia alaskana has also been mistaken for *Asahinea chrysantha* (Tuck.) Culb. & Culb. which occurs in the same region and the two species can probably be found together in the field. *Cetrelia alaskana* always has some rhizines on the lower surface even though they may not be produced in abundance while the lower surface of *A. chrysantha* is invariably naked. *Asahinea chrysantha* also contains usnic acid in the upper cortex and is consequently yellow-colored in contrast to the usnic acid-lacking, tan-colored upper cortex of *C. alaskana*. The

medulla of *A. chrysantha* contains alectoronic acid and is consequently strongly fluorescent in ultraviolet light while the medulla of *C. alaskana* contains imbricaric acid and is not fluorescent. A detailed account of *Asahinea* and its relationships to other groups in the Parmeliaceae has already been given (W. L. Culberson and C. F. Culberson, 1965).

CHEMICAL ANALYSIS.—All 14 samples of *C. alaskana* tested microchemically contained atranorin and imbricaric acid. The identity of imbricaric acid was definitely established by the extraction and detailed analysis of a small sample (C. F. Culberson and W. L. Culberson, 1966). The substance responsible for the KC+ reaction observed on the thallus could not be identified.

ADDITIONAL SPECIMENS EXAMINED:

U.S.A.: ALASKA: Pitmegea River, 15 mi. upstream from Cape Sabine, 68°48′N, 154°20′W, *Thomson, Lich. Arct.* 13. (Type collection, see above.) Ogotoruk Creek Drainage, 68°05′N, 165°32–47′W, *Johnson et al.* 21 (COLO). 40 mi. east of Cape Lisburne, *Cantlon & Gillis* 57–136A (MSC). Kuskakwin, Goodnews Bay, *Geist,* 1933 (Herb. Degelius, LD). Lower Telephone Creek, *Palmer* 585 (US, WIS). Peace River, *Palmer* 614 (US, WIS).

2. Cetrelia braunsiana (Müll. Arg.) Culb. & Culb., comb. nov. PLATE 15

Parmelia braunsiana Müll. Arg., Flora 64:506. 1881. Type: Japan, Tokyo, *Brauns* 2 (*pro parte*) (G, holotype).

Platysma braunsianum (Müll. Arg.) Hue, Nouv. Arch. Mus., IV, 1:210. 1899.

Cetraria braunsiana (Müll. Arg.) Zahlbr., Bot. Mag. [Tokyo] 41:353. 1927.

Parmelia braunsiana f. *isidiosa* Müll. Arg., Flora 64:506. 1881. Type: Japan, Tokyo, *Brauns* 2 (*pro parte*) (G, holotype).

Platysma braunsianum f. *isidiosum* (Müll. Arg.) Hue, Nouv. Arch. Mus., IV, 1:210. 1899.

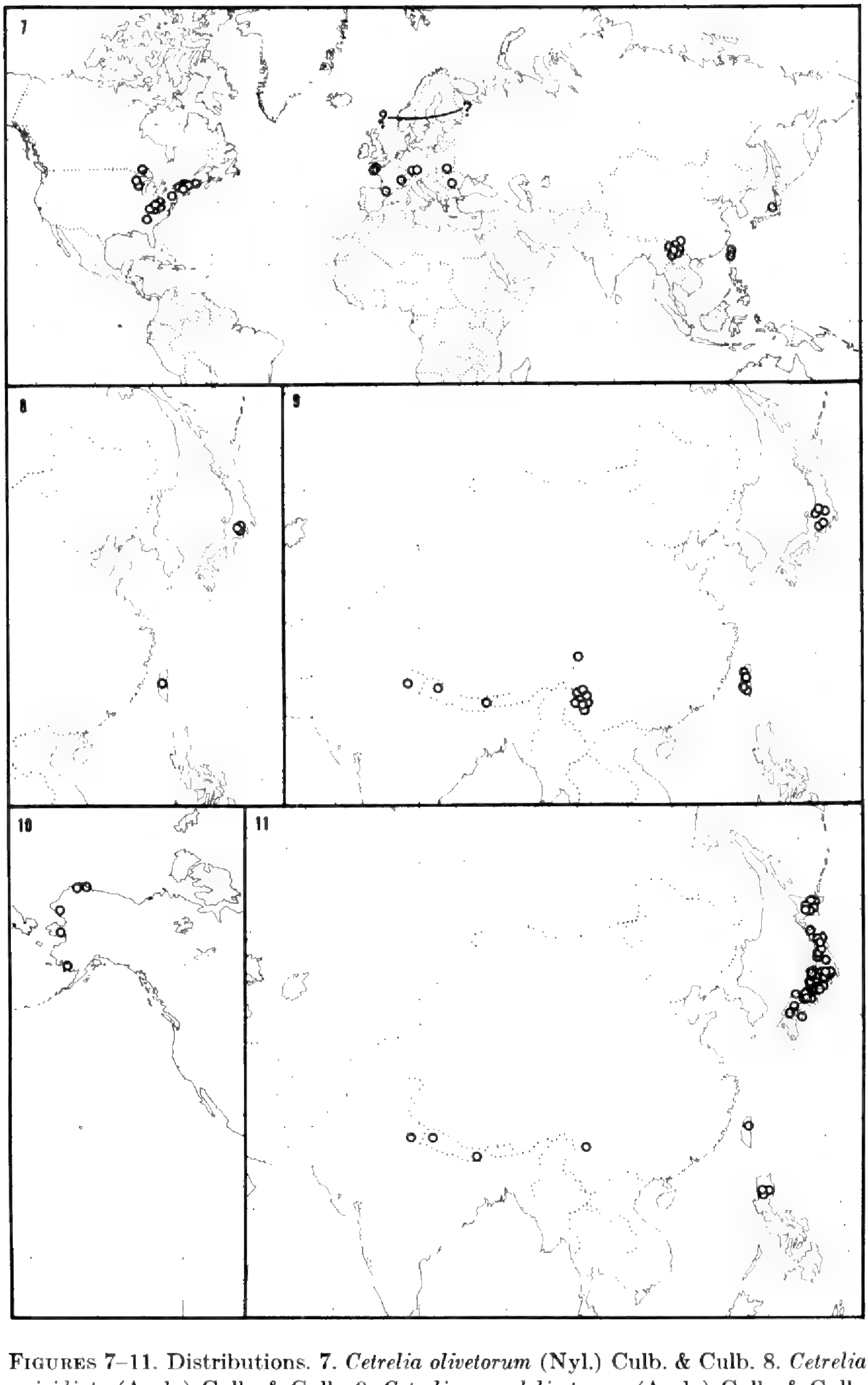
Cetraria braunsiana f. *isidiosa* (Müll. Arg.) Zahlbr., Catal. Lich. Univ. 6:284. 1930.

C. collata f. *isidiata* Asah., Journ. Jap. Bot. 10:475. 1934. Type: Japan, Musashi Prov., Mt. Buko, *Asahina* 71b (TNS, lectotype).

Thallus medium to large, 12–24 cm. broad; lobes 0.5–1.7 cm. broad. Upper surface gray or ashy-white, uniformly brownish or tan in old herbarium specimens, the margins ± ascendent and commonly isidiate, at least in part, the tips pruinose, pseudocyphellate, the pores small, punctiform to irregular, rarely more than 1 mm. broad, often associated with tiny, granular, delicately coralloid isidia. Lower surface black, the margins brown or grayish like the color of the upper surface, not punctate; rhizines black. Upper cortex 19–25μ thick; medulla 109–264μ thick; lower cortex 16–22μ thick. Apothecia rare, submarginal, perforate, about 0.5 mm. broad; hymenium 93–109μ thick; subhymenial layers 40–53μ thick, underlain by a dense layer of algae. Spores 8, ovoid, 12–15×8–9μ. Pycnidia rare, marginal, black, pruinose; conidia 1×4–6μ, rod-shaped, the ends slightly enlarged.

MEDULLARY REACTIONS.—K−, C−, KC+ pink, PD−.

CONSTITUENTS.—Alectoronic and α-collatolic acids and atranorin.



FIGURES 7–11. Distributions. 7. *Cetrelia olivetorum* (Nyl.) Culb. & Culb. 8. *Cetrelia isidiata* (Asah.) Culb. & Culb. 9. *Cetrelia pseudolivetorum* (Asah.) Culb. & Culb. 10. *Cetrelia alaskana* (Culb. & Culb.) Culb. & Culb. 11. *Cetrelia braunsiana* (Müll. Arg.) Culb. & Culb.

DISTRIBUTION (Map, Fig. 11).—Widespread in Hokkaido and Honshu, Japan, in the high mountains of Formosa, Luzon, Philippines, Yunnan, China, and in the Himalayas; on tree trunks and over boulders.

Cetrelia braunsiana, *C. chicitae*, and *C. nuda* have been recognized in recent years by Japanese botanists as *Cetraria collata* f. *isidiata* Asah., *C. collata* sens. str. (=f. *collata*), and *C. collata* f. *nuda* Hue respectively. They are, however, quite distinct morphologically, although chemically all produce atranorin and alectoronic and α-collatolic acids. *Cetrelia braunsiana* is isidiate, *C. chicitae* is sorediate, and *C. nuda* produces neither soredia nor isidia, but it has pseudocyphellae different from those of the other two species.

The differences among these three species, and the consequent justification for regarding them as distinct and of specific rank are summarized in Table 5.

TABLE 5.—*The percentages of Japanese specimens of* Cetrelia braunsiana, C. chicitae, *and* C. nuda *showing various morphological traits and the geographic distribution of the species*

	braunsiana	*chicitae*	*nuda*
Total number of specimens examined	74	35	51
Small pseudocyphellae (less than 1 mm.)	93	100	10
Large pseudocyphellae (more than 1 mm.)	7	0	90
Isidia	100	0	0
Soredia	0	100	0
Apothecia	4	17	83
Pycnidia	7	14	100
Pycnidia pruinose	0	0	24
Lobes pruinose (at least in part)	69	43	14
Lower surface punctate	1	6	59
Japanese range	Hokkaido, Honshu	Hokkaido, Honshu	Southern Honshu, Shikoku, Kyushu

Japanese specimens belonging to this group never produce both isidia and soredia and most (90%) of the specimens with neither isidia nor soredia have large pseudocyphellae rather than the small ones characteristic of the other two species. It should be pointed out, however, that the isidia in *Cetrelia braunsiana* are often produced in very small numbers. Invariably, however, if Japanese specimens belonging to this group and having small pseudocyphellae and no soredia are examined carefully under the dissecting microscope, at least a few

delicate marginal isidia will be found. The type specimen itself of *C. braunsiana* has very few isidia.

It is apparent from Table 5 that *Cetrelia braunsiana* and *C. chicitae* are more similar to each other than they are to *C. nuda*. The nonisidiate, esorediate *C. nuda* always produces pycnidia, which are often pruinose, and commonly has apothecia and a punctate lower cortex. It actually belongs to the *Cetrelia sanguinea* group and is not particularly closely related to *C. braunsiana* and *C. chicitae* at all, although its taxonomy has been confused with theirs.

As pointed out above, it is generally possible to distinguish Japanese specimens of *Cetrelia braunsiana* from those of *C. chicitae* by careful examination of the plants for isidia. Farther south, and especially in the Philippines, the distinctions may become more difficult. In some Philippine specimens the margins of the lobes are densely covered with soredia-like structures that become isidioid and granular, apparently by compaction and the formation of a cortexlike surface. These anomalous specimens are otherwise well developed and may represent a unique local race even though essentially typical specimens of both *C. braunsiana* and *C. chicitae* are also known from the Philippines. This local problem in distinguishing between some specimens of *C. braunsiana* and *C. chicitae*, however, should not be taken to indicate that these two species differ only slightly because in reality they differ quantitatively in the expression of many traits (Table 5). Nevertheless, the identification of certain isolated specimens from the Philippines may depend entirely upon the presence of isidia as opposed to soredia.

The type specimen of *Parmelia braunsiana* Müll. Arg. is isidiate and the type of *P. braunsiana* f. *isidiosa* Müll. Arg., really part of the same collection, is somewhat more isidiate. In view of the great variation in the production of isidia in the Japanese population of this species, there is no basis for recognizing the forma.

Cetrelia braunsiana is part of the Sino-Japanese floristic element with a range extension into Formosa and the Philippines. In spite of its relatively close relationship to the very widespread species *C. chicitae*, no specimens of it from outside the Orient are known. In Japan *C. braunsiana* is widely distributed and is found at lower elevations as well as in the mountains. Its broader amplitude of ecologic tolerance, as compared to that of most of the Japanese species of *Cetrelia*, is also seen in its general abundance in Japan as well as in its more extensive vertical geographic range there.

CHEMICAL ANALYSIS.—Alectoronic acid, α-collatolic acid, and atranorin were identified in the 32 samples tested. The tests were made without difficulty and, in most cases, directly on the acetone extract, the concentration of α-collatolic acid being sufficient to give a good

chromatogram. Although many of the residues were yellow, no known pigment could be identified and all tests for usnic acid were negative.

NOMENCLATURE.—In the Japanese botanical literature the name *Cetraria braunsiana* (Müll. Arg.) Zahlbr. has been used consistently to refer to the species treated here as *Platismatia interrupta* Culb. & Culb. A simple but widespread misunderstanding of the application of the name apparently accounts for this.

This species was named for David Brauns (1827–1893), Professor of Geology at the University of Halle, who made the original collection near Tokyo in 1881.

REPRESENTATIVE SPECIMENS EXAMINED:

JAPAN: HOKKAIDO: Sapporo, *Faurie* 9212 (PC). Prov. Ishikari: Daisetsu, Kuro-dake, *Asahina*, 1937 (TNS, two collections); Hot Spring Matsuyama, *Asahina*, 1935 (TNS). Prov. Kitami: Lake Abashiri, *Asahina & Togashi*, 1953 (TNS). Prov. Kushiro: Lake Akan, *Asahina*, 1953 (TNS).

HONSHU: Hirosaki, *Faurie* 196 (PC). Prov. Bingo: Sera-gun, Kamiyama-mura, *Sato*, 1932 (TNS). Prov. Echigo: Iwafune-gun, Arakawa-cho, *Togashi*, 1956 (TNS). Prov. Echizen: Imadate-gun, Okamoto-mura, *Hosoi & Ui*, 1935 (TNS). Prov. Ettyu: Magawa Pass, *Asahina*, 1936 (TNS, two collections). Prov. Harima: Shiso-gun, Mikawa-mura, Funakoshi, *Utsumi*, 1951 (TNS). Prov. Inaba: Karo, *Ikoma*, 1953 (TNS). Prov. Iwaki: Matsukawa-ura, *Kurokawa* 58086, 58087 (TNS). Prov. Iwashiro: Ura-bandai, *Asahina*, 1954 (TNS). Prov. Izu: Nirayama, Honryu-ji Temple, *Asahina*, 1956 (TNS). Prov. Kaga: Enuma-gun, Hot Spring Yamanaka, *Togashi*, 1959 (TNS). Prov. Kai: Mt. Minobu, *Togashi*, 1961 (TNS, three collections). Prov. Kii: Mt. Koya, *Numajiri* 699 (TNS). Prov. Kozuke: Tano-gun, Ueno-mura, Shio-no-sawa Pass, *Togashi*, 1956 (TNS). Prov. Mikawa: Mt. Horaiji, *Asahina*, 1956 (TNS, two collections). Prov. Mino: Seki-ga-hara, *Asahina*, 1938 (TNS). Prov. Musashi: Chichibu, Ryogami-mura, Hyugaotani, *Kurokawa* 550534 (TNS); Mt. Buko, *Asahina* 71b (TNS). Prov. Owari: Inuyama, *Asahina*, 1938 (TNS). Prov. Rikuchu: Isawa, Mt. Shishihana, *Suzuki* 491 (TNS). Prov. Rikuzen: Tamatsukuri-gun, Naruko-cho, *Asahina & Togashi* (TNS). Prov. Sagami: Odawara, Mt. Daiyuzan, Saijo Temple, *Togashi*, 1956 (TNS). Prov. Settsu: Arima-gun, Dojo-mura, *Togashi*, 1952 (TNS). Prov. Shimotsuke: Nikko, Lake Yuno-ko, *Asahina*, 1931 (TNS, two collections). Prov. Shinano: Lake Shirakaba, *Asahina & Togashi*, 1958 (DUKE); Mt. Kimpu, *Asahina, Togashi & Nuno* (TNS, 2 collections); Suwa-gun, Izumino-cho, *Asahina & Togashi*, 1958 (TNS); Mt. Yatsu-ga-take, Hot Spring Shibu-no-yu, *Kurokawa* 58198 (TNS) and 58199 (DUKE); Mt. Tadeshina, *Kurokawa* 51746, 71864, 58374, 58375 (TNS) and 58375 (MSC); Mt. Norikura, *Asahina*, 1952 (TNS). Prov. Suo: Hikarishi, Murozumi, *Asahina & Togashi*, 1959 (TNS). Prov. Suruga: Lake Saiko (Nishi-no-umi) near Mt. Fuji, *Culberson & Culberson* 10684 (DUKE). Prov. Tango: Miyazu-shi, Nariai Temple, *Togashi*, 1956 (TNS). Prov. Uzen: Goshiki-numa, *Suzuki*, 1954 (TNS). Prov. Wakasa: Mt. Aoba, *Togashi*, 1956 (TNS). Prov. Yamashiro: Atago-gun, Hanaze-mura, Mt. Taihi, *Togashi*, 1955 (TNS).

SHIKOKU: Prov. Tosa: Hata-gun, Okata-cho, *Kurokawa* 550231, 550232 (TNS); Mt. Yokogura, *Fujikawa*, 1931 (TNS).

FORMOSA: Mt. Ali, 2,200 m., *Kurokawa* 13 (TNS). Mt. Ba-Hsen, 2,180 m., *Jen-rong Wang* 133 (DUKE). Piyanan Pass, 1,600–1,900 m., *Kurokawa* 821 (TNS).

PHILIPPINES: LUZON: Benguet Prov.: Mt. Pulog, *McGregor*, 1909 (TUR). Mountain Prov.: Mt. Data, *Hale* 26019, 26150, 26401 (US).

CHINA: YUNNAN: Kou-toui, above Mo-so-yn,[2] *Delavay* 3009 (PC).

NEPAL: Mewakhola Valley, 11,000 ft., *Awasthi* 2265 (UPS). Above Sauwala Khola, 10,500 ft., *Stainton et al.* 4379b (*pro parte*) (BM).

INDIA: Northwestern Himalayas: Kamaon, Almora District, Dhakuri Ridge, 9,500 ft., *Awasthi & Awasthi* 633 (UPS).

3. Cetrelia cetrarioides (Del. ex Duby) Culb. & Culb., comb. nov. PLATE 15

Parmelia perlata β cetrarioides Del. ex Duby, Bot. Gall., ed. 2, 601. 1830. Type: France, Mont d'Or, *Delise*, 1828 (STR, lectotype). The lectotype, designated by Hale (1960), was not seen, but an extract of a fragment of it prepared by Hale was studied microchemically by us (see below).

P. cetrarioides (Del. ex Duby) Nyl., Flora 52:289. 1869.

P. monochorum Zahlbr., Symb. Sin. 3:191. 1930. Type: China, Szechwan, Döko Pass southwest of Muli, *Mazzetti* 7399 (WU, holotype).

P. cetrarioides f. *bisoralifera* Laven, Repert. Spec. Nov. Fedde 50:294. 1941. Type: Bavaria, prope lacum Lautersee, *Laven* (not seen).

Thallus medium to large, 7–16 cm. broad; lobes (0.5–)1–1.5 cm. broad. Upper surface uniformly tan or pale, pseudocyphellate, the pores very small, rarely reaching 0.5 mm., the margins of the lobes finely and usually abundantly sorediate. Lower surface jet-black, the margins brown, usually punctate with many small pores; rhizines few, black, rarely pale. Upper cortex (16–)19–28(–31)μ thick; medulla (62–)90–155(–171)μ thick; lower cortex 16–25(–28)μ thick. Apothecia extremely rare, 1–2 mm. broad (immature, the only ones seen *in situ*). Spores ovoid, 12–14×19–24μ (seen in a single apothecial fragment). Pycnidia unknown.

MEDULLARY REACTIONS.—K−, C−, KC− or KC+ pinkish, PD−.

CONSTITUENTS.—Perlatolic or imbricaric acid and atranorin.

DISTRIBUTION (Maps, Figures 12–13).—Eastern North America, Japan, the mountains of southern Asia, and western Europe; usually in shady places, on the bark of trees, rock faces, and over boulders.

The *Cetrelia cetrarioides* complex includes four chemically distinct populations. The population producing atranorin and olivetoric acid in the medulla is slightly but distinctly different morphologically from the other three and clearly represents a different taxon, here treated as the species *Cetrelia olivetorum* (see page 515). The remaining three chemical types consist of plants which produce atranorin and (1) perlatolic acid, (2) imbricaric acid, or (3) alectoronic and α-collatolic acids. In examining a large series of herbarium specimens one may be tempted to see subtle morphological "tendencies" among the chemical races, but the accurate identification of individual specimens ultimately depends upon chemical analysis.

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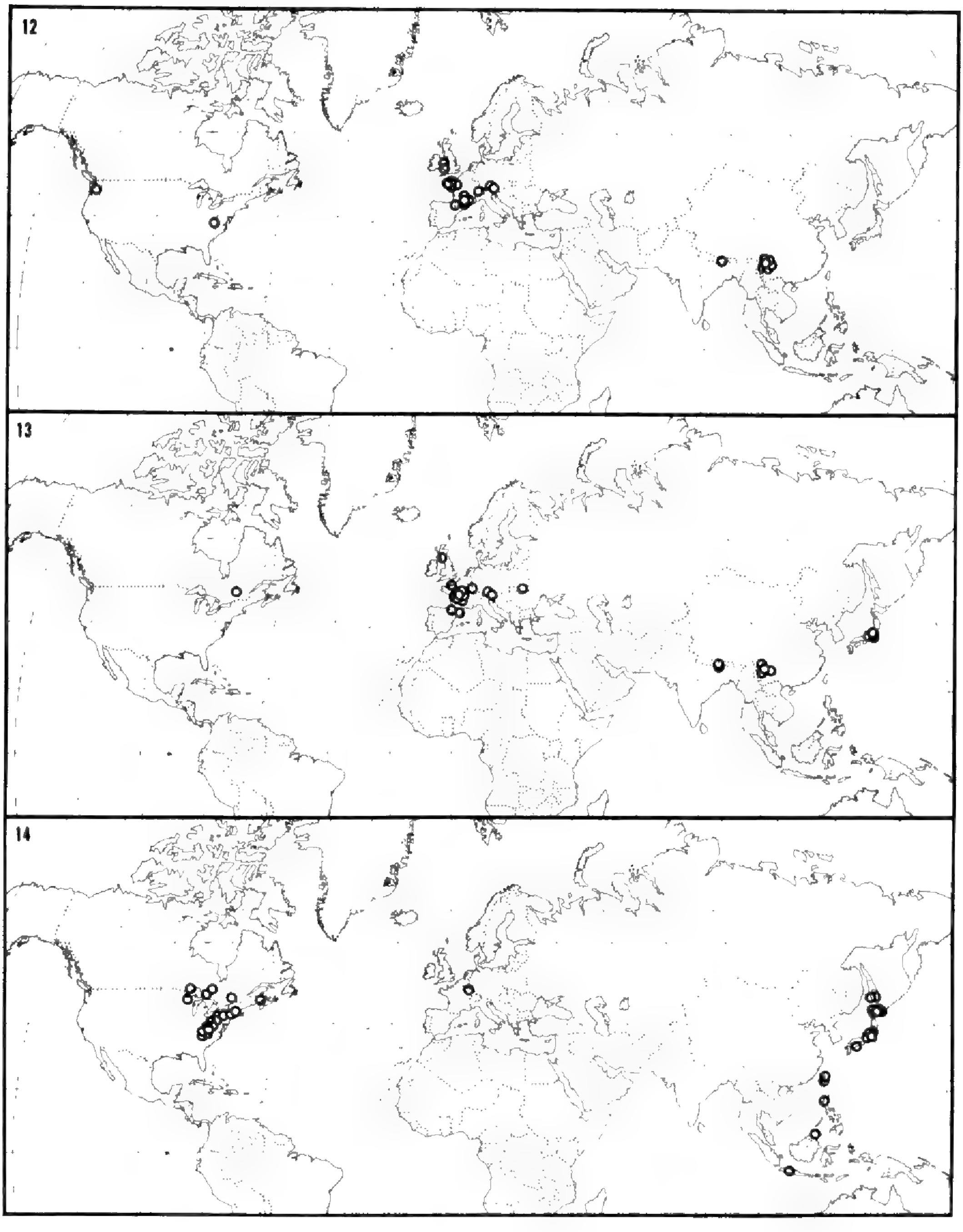
[2] The spelling of Chinese place names in the citation of specimens taken by Delavay follows Bretschneider's (1898) excellent summary of Delavay's botanical work. Our only modification of Bretschneider's spellings has been to hyphenate compound names.



FIGURES 12–14. Distributions. 12–13. *Cetrelia cetrarioides* (Del. ex Duby) Culb. & Culb. (two chemical strains). 12. *Cetrelia cetrarioides* (Del. ex Duby) Culb. & Culb. sens. str., the strain with perlatolic acid. 13. *Cetrelia cetrarioides* (Del. ex Duby) Culb. & Culb. sens. lat., the strain with imbricaric acid. 14. *Cetrelia chicitae* (Culb.) Culb. & Culb.

In the present study the plants containing alectoronic and α-collatolic acids are assigned to *Cetrelia chicitae* and the perlatolic and imbricaric acid-containing plants to *C. cetrarioides* sens. lat. It may be thought arbitrary and untenable, in the absence of a unique morphology, to consider the plants that produce alectoronic and α-collatolic acids to represent a distinct species while keeping together taxonomi-

cally those that produce perlatolic acid and those that produce imbricaric acid. As pointed out in a previous study of the chemistry and geographic distribution of the components of the *cetrarioides* complex (Culberson, 1958), plants assigned to *C. chicitae* represent the bulk of the *P. cetrarioides* complex in North America, while in Europe the complex is made up almost entirely of perlatolic and imbricaric acid-producing populations. While the three chemical races might be nearly sympatric purely from the point of view of qualitative range (although the worldwide distribution here is poorly known), the quantitative distributions are clearly different. For this reason and since the production of the two compounds alectoronic acid and α-collatolic acid seems to be a relatively large departure from the chemistry of the other chemical types, this type is regarded as a distinct species.

The retention of the remaining two types, the perlatolic acid-containing plants and the imbricaric acid-containing ones, within the single species *Cetrelia cetrarioides* is less satisfactory. Unlike the chemical species *C. chicitae*, these two races do not seem to be significantly more abundant in one part of their range than in other parts. Although by proper chemical analyses it is possible to identify which of the acids is present in a given specimen, there are a few imbricaric acid-containing specimens in which our microchemical and chromatographic tests cannot assure with absolute certainty the absence of perlatolic acid (although an alternate explanation is possible; see the chemical discussion below). In view of the essentially sympatric distribution of these two chemical types and the possibility at least that some individuals may actually produce both perlatolic and imbricaric acids, it does not seem desirable at present to try to accommodate the chemical variation in the taxonomy.

Some nonchemical aspects of the taxonomy in the *Cetrelia cetrarioides* complex are also still not completely explored. For example, two anomalous, well developed, imbricaric acid-producing specimens from Sikkim in the Himalayas, where the genus *Cetrelia* is exceptionally well represented, lacked soredia altogether. The plants are relatively small-lobed and by habit alone are obviously closely allied to *C. cetrarioides*. Since typical specimens of the imbricaric acid-producing race of *C. cetrarioides* are found in the same Himalayan region, these specimens have provisionally been assigned to *C. cetrarioides* in spite of their lack of soredia. They are pointed out here only to call attention to the fact that additional studies on new collections of the *C. cetrarioides* complex from the Himalayas might necessitate additional modifications in the taxonomy.

The tundra-inhabiting species *Cetrelia alaskana* might be mistaken for *C. cetrarioides* because superficially it looks similar. Like many individuals of *C. cetrarioides*, *C. alaskana* produces imbricaric acid, but

it is never sorediate while soredia are usually well developed in most specimens of *C. cetrarioides*. The two species also have strikingly different ecologies, and their geographic ranges are widely separated.

The soredia in *Cetrelia cetrarioides* are typically confined to the margins of the lobes in long soralia. An anomalous form with conspicuous capitate soralia has been named as an infraspecific variation (Laven, 1941). An analogous form bearing capitate soredial masses has also been described for *Platismatia norvegica*. These rare, peculiar forms are not considered taxonomically in this study because they seem to represent pathological rather than natural growths.

In its broad sense, including both the chemical races that compose it, *Cetrelia cetrarioides* is the most widely ranging species in the genus. It is, of course, the very fact of this broad range and the accompanying internal chemical variation that would speak against considering *C. cetrarioides* a single species as it is regarded in the present study.

Cetrelia cetrarioides, like the closely related species *C. olivetorum* and *C. chicitae*, is generally restricted to places with relatively moist, cool climates. It is probably most abundant and best developed in the British Isles and in other oceanic parts of western Europe. As would be expected, the southernmost stations of its range on all continents are in mountains.

Throughout much of its range *Cetrelia cetrarioides* is very infrequent. Its extreme rarity in North America has already been reported (Culberson, 1958), a rarity all the more noteworthy in view of the extreme local abundance of the closely related species *C. chicitae* (see the discussion for that species). In parts of Europe *C. cetrarioides* is also very rare. For example, in the southern parts of Norway (Lynge, 1921), Sweden (Du Rietz, 1924), and Finland (Hakulinen, 1963)—regions which have been intensively explored by lichenologists—it has been found in only a few localities.[3] In Asia too the records are widely scattered. The extreme rarity of the species of course means that it has often gone unnoticed by collectors. The distribution maps given here (Figures 12–13) are consequently only roughly approximate.

CHEMICAL ANALYSIS.—Sixty-nine samples of this species were tested; 35 contained atranorin and perlatolic acid and 34 contained atranorin and imbricaric acid mixed with at least one unidentified phenolic substance. Perlatolic acid was identified by the crystals observed in the

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[3] No Scandinavian specimens of *Cetrelia cetrarioides* were seen in this study. Although the species unquestionably occurs in southern Scandinavia, no localities are given on the maps (Figures 12–13) because the chemical race to which such specimens belong is unknown. The presence of *C. cetrarioides* sens. lat. in Scandinavia is acknowledged on the map in Figure 1 which shows the geographic distribution of species numbers in the genus *Cetrelia*. The two species recorded there for Scandinavia are *C. cetrarioides* and *C. olivetorum*.

GE and GAW solutions and by the straight extinction of these crystals with crossed Nicols. Imbricaric acid crystals show oblique extinction and a somewhat different morphology in these solutions.

All residues were chromatographed in NH_4OH-n-butanol, and many of them were hydrolyzed with 0.1 N Na_2HPO_4 to detect imbricaric acid. While perlatolic acid-containing samples were always KC— (with the possible exception of one specimen), a definite to pale KC+ red reaction was observed on many imbricaric acid-containing thalli. Imbricaric acid was identified by comparison with imbricaric acid in *Cetrelia alaskana* (C. F. Culberson and W. L. Culberson, 1966). A KC+ reaction which has also been observed with *C. alaskana* is due to an unidentified KC+ substance or to a low concentration of some C+ substance. Further studies are necessary to identify this material.

Asahina and Fuzikawa (1935) have suggested that imbricaric acid and perlatolic acid may occur together, but their evidence is not conclusive. Hydrolysis of several imbricaric acid-containing residues showed a spot by chromatography at an R_f corresponding to that for olivetol-2-carboxylic acid. This could be explained if perlatolic acid were also present, but such a mixture would still not be KC+. Either the samples containing imbricaric acid may also contain perlatolic acid and still a third constituent to give the KC+ reaction, or these samples contain imbricaric acid and a KC+ substance that produces olivetol-2-carboxylic acid upon hydrolysis.

NOMENCLATURE.—After a careful study of the appropriate specimens from Delise's herbarium, Hale (1960) was able to typify *Parmelia perlata β cetrarioides* Del. ex Duby in the sense that the binomial *P. cetrarioides* (Del. ex Duby) Nyl. has generally been used. Although we were not able to examine the lectotype, Hale's (1960) photograph of it is unmistakable. From a microextract that he had made from it at the time of his study and which he subsequently gave to us for testing, we confirmed his report that this specimen contains perlatolic acid. In the quite possible eventuality that a future interpretation based on additional evidence should recognize the imbricaric acid-producing race as a distinct species, it should be noted that *P. monachorum* Zahlbr. offers apparently the oldest specific epithet for this variation; we have identified imbricaric acid and atranorin in the holotype.

Santesson (1942) noted that *Pseudoparmelia pseudofallax* Gyeln. is also a synonym of "*Parmelia cetrarioides*," but we have not seen the type specimen and do not know to which chemical race it belongs. Even if it belongs to the variant producing imbricaric acid, it could not be used, since the epithet *monachorum* is older.

ADDITIONAL SPECIMENS EXAMINED:

Specimens of *C. cetrarioides*, the perlatolic acid-producing race:

U.S.A.: West Virginia: Pendleton Co.: Panther Knob, *Hale* 14264 (DUKE). Washington: Snohomish Co.: Marysville, *Grant*, 1926 (MICH), 1927 (MICH).
CHINA: Yunnan: Kou-toui, above Mo-so-yn (Lan-kong), 3,000 m., *Delavay* 1887 (PC); Yen-tze-hay, 300 m., *Delavay*, 1887 (PC); Yen-tze-hay, Lan-kong. *Delavay*, s.d. (PC); Koua-la-po, *Delavay* 1595 (*pro parte*) (PC); Koua-la-po, Ko-kin, 3,000 m., *Delavay*, 1885 (PC, 2 collections).
SIKKIM: Tonglo, 10,000 ft., *Hooker* 2083 (K).
POLAND: Mont. Carphatica, Mont. Gorganae, near Skole, *Aasamaa* Cet-302 (DUKE).
AUSTRIA: Hallstadt, *ex herb. Bory de St-Vincent*, 1805–1806 (PC).
GERMANY: Bayern: Obere Hochebene, Wornbrunn, *Schwind*, 1925 (BP).
SWITZERLAND: Vaugeron, near Genève, *Schleicher* 80 (DUKE). Ticino: Fusio, Maggia Valley, *Barkman* 4290 (DUKE).
FRANCE: Côtes-du-Nord: Forêt de Lorges, *des Abbayes*, 1929, 1930 (Herb. des Abbayes, 2 collections).
Finistère: Forêt de Coatloc'h, *Piquenard*, 1900 (PC); the same, *des Abbayes*, 1930, 1933 (Herb. des Abbayes, 2 collections).
Aveyron: Forêt de Serre, *Barreau*, 1831 (PC, 3 collections).
Sarthe: Forêt de Perseigne, *des Abbayes*, 1936 (Herb. des Abbayes).
Vosges: Docelles, *Harmand, Lich. Loth.* 288 (*pro parte*) (PC).
Puy-de-Dôme: Bois de Job, near Ambert, *Gasilien*, 1883 (Herb. des Abbayes).
Hautes-Pyrénées: Pauze, near Cauterets, collector unknown (PC).
WALES: Merionethshire: Penmaenpool, *Culberson & Culberson* 11564 (DUKE).

Specimens of *C. cetrarioides* sens. lat., the imbricaric acid-producing race:

CANADA: Québec: Labelle Co.: North of La Conception, *Hermann* 15783 (DUKE).
JAPAN: Fujiyama; Ityigome-Magajisi, *Almquist*, 1879 (S); the same, Umaga-yeshi, *Almquist*, 1879 (S). Togakushi, *Faurie* 777 (PC).
CHINA: Yunnan: Hee-chan-men, *Delavay*, 1887 (PC); Santo-ha-ho, 3,000 m., *Delavay*, 1888 (PC, 2 collections); Lenago Pass between Mekong and Yangtse, 27°43′N, *Gebauer*, 1914 (W). Szechwan: Döko Pass SW of Muli, *Handel-Mazzetti* 7399 (UW).
SIKKIM: Lachan, 13,000 ft., *Hooker* 2086 (K). Wallanchoon 13,000 ft., *Hooker* 1814, 2082 (K).
POLAND: Mont. Carphatica, Mont. Gorganae, near Skole, *Aasamaa* Cet-301 (DUKE).
GERMANY: München, *Arnold, Lich. Monac. Exs.* 324a, (*pro parte*), 324b, (*pro parte*) (PC).
CZECHOSLOVAKIA: Nízke Poloniny, Nová Sedlica, *Pišút, Lich. Slovak. Exs.* 13 (DUKE).
FRANCE: Calvados: Forêt de St-Tever, collector unknown, 1890 (PC).
Seine-et-Marne: Fontainebleau, *Nylander*, s.d. (PC).
Puy-de-Dôme: Besse, *des Abbayes*, 1933, 1935 (Herb. des Abbayes, 2 collections).
Haute-Vienne: Montagnes de Goullet, *Lamy de la Chapelle*, 1874 (PC); Goullet, bei St. Sylvestre, *Lamy de la Chapelle*, as *Arnold, Lich. Exs.* 582 (PC).
Pyrénées-Orientales: La Massane, *des Abbayes*, 1933 (Herb. des Abbayes).
Hautes-Pyrénées: Pauze, near Cauterets, collector unknown, s.d. (PC).
SCOTLAND: Argyllshire: Ardnamurchan Peninsula, Salen, *Culberson & Culberson* 11816 (DUKE).

4. Cetrelia chicitae (Culb.) Culb. & Culb., comb. nov. PLATE 14

Cetraria chicitae Culb., Bryologist 68:95. 1965. Type: U.S.A., West Virginia, *Hale, Lich. Amer. Exs.* 56 (DUKE, holotype).

Thallus medium to large, 10–16 cm. broad; lobes 0.7–1.7 cm. broad. Upper surface light gray or ashy, uniformly brown or tan in old herbarium specimens, smooth, often pruinose at the tips, the margins erupting with fine soredia, pseudocyphellate, the pores small, rarely exceeding 1 mm. Lower surface jet-black, the margins brown or colored like the upper surface and in some specimens wrinkled, the crests of the folds becoming punctate. Upper cortex 16–26(–31)μ thick; medulla 85–186(–260)μ; lower cortex, 10–26μ thick. Apothecia very uncommon, perforate, 4–5 mm. broad; hymenium 62–78μ thick; subhymenial layers 62–78μ thick. Mature spores unknown. Pycnidia rare, marginal; conidia 1$\times$5–6μ, rod-shaped, the ends somewhat enlarged.

MEDULLARY REACTIONS.—K−, C−, KC+ pink, PD−.

CONSTITUENTS.— Alectoronic acid and α-collatolic acid and atranorin.

DISTRIBUTION (Map, Figure 14).—Southern Ontario and New Brunswick, Canada, and the adjacent United States, south in the Appalachian Mountains to North Carolina; southern Sakhalin and Japan, and the mountains of Formosa, Luzon (Philippines), Sabah (Borneo), and Java; on the trunks of trees and on rocks and over boulders. A discussion of the range of this species is included in the treatment for *C. cetrarioides* (p. 501).

Cetrelia chicitae is essentially indistinguishable morphologically from *C. cetrarioides*, although the species differ in chemical constituents and in their geographic distributions. For a full discussion of the relationship of *C. chicitae* to *C. cetrarioides* and to *C. olivetorum*, see the treatment of *C. cetrarioides* (p. 498). The relationship of *C. chicitae* to other species of the same chemistry for which it might be mistaken is explained in the taxonomic discussion of *C. braunsiana* (pp. 495–496).

CHEMICAL ANALYSIS.—The 24 samples tested all contained atranorin, alectoronic acid, and α-collatolic acid. Early in the study, 14 of these specimens were tested by means of a single acetone extraction, but later the method of double extractions with benzene and then acetone was employed. Microcrystal tests in the GE, GAW, and GA*o*-T solutions were always confirmed by chromatography to prove the presence of α-collatolic acid. In the fragments tested the concentrations of all three substances were always sufficient to give a good test without the difficulties sometimes encountered in other species in demonstrating small concentrations of α-collatolic acid or atranorin in the presence of alectoronic acid.

ADDITIONAL SPECIMENS EXAMINED:

U.S.A. AND CANADA: For a long list of selected specimens examined, see the original description of this species (W. L. Culberson, 1965).

U.S.S.R.: SAKHALIN ISLAND: Takinosawa, *Asahina*, 1932 (TNS, 2 collections); Aikawa, *Asahina*, 1932 (TNS).

KOREA: Locality unknown, *Asahina*, 1934 (TNS).

JAPAN: For a complete list of the Japanese specimens examined at the time that the species was described, see W. L. Culberson (1965).

FORMOSA: Mt. Ali, 2,200 m., *Kurokawa* 12, 38 (TNS); Mt. Shin-Kao-San, Mt. Chien-San, 3,100–3,300 m., *Kurokawa* 251 (TNS).

SABAH: Kinabalu National Park, near East Mesilau River, 1,700 m., *Hale* 28431 (US).

PHILIPPINES: MOUNTAIN PROV.: Mt. Data, 2,312 m., *Hale* 26358 (US).

JAVA: Res. Pasoeroean, Goenoeng Ardjoena, Tretes-Lalidjiwa-track, *Du Rietz* 95:15 (UPSV).

FRANCE: VOSGES: Docelles, l'Encerf, *Harmand, Lich. Loth.* 288 (DUKE, PC).

5. **Cetrelia collata** (Nyl.) Culb. & Culb., comb. nov.

Platysma collatum Nyl., Flora 70:134. 1887. Type: China, Yunnan, *Delavay* 1590 (H-Herb. Nyl. No. 36116a, holotype).

Cetraria collata (Nyl.) Müll. Arg., Nouv. Giorn. Bot. Ital. 24:192. 1892.

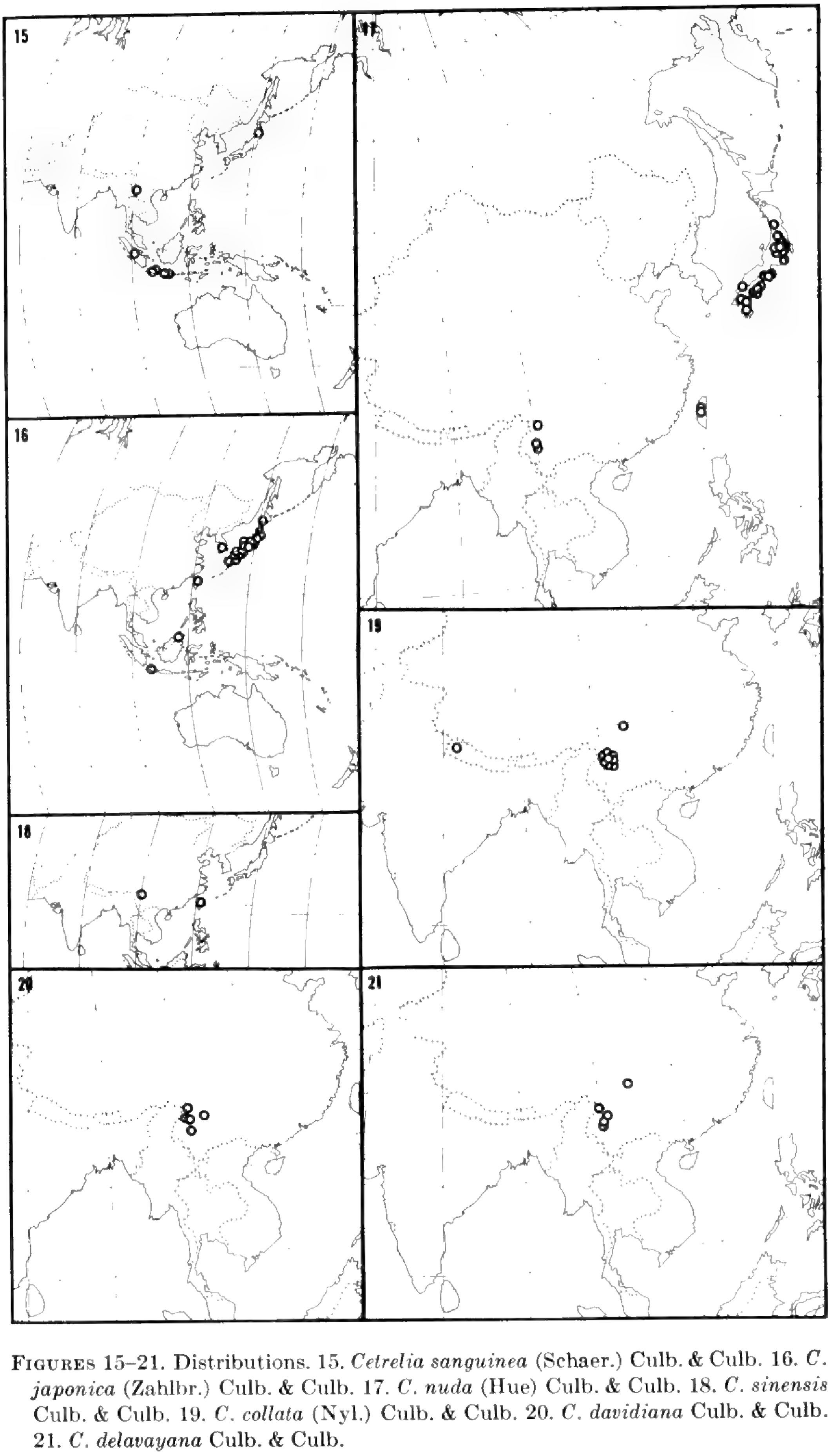
Thallus medium, to 15.0 cm. broad; lobes 0.8–2.5 cm. broad. Upper surface pale brownish in old herbarium specimens (whitish when fresh?), smooth, pseudocyphellate, the pores large, many becoming confluent and exceeding 1 mm. Lower surface jet-black, punctate in some specimens, the margins dark brown or colored like the upper surface, relatively smooth, ascendent; rhizines few. Upper cortex 16–34μ thick; medulla 109–264μ thick; lower cortex 16–25μ thick. Apothecia 0.7–2.0 cm. broad, cup-shaped at first and expanded with age, perforate or entire, the thalloid exciple wrinkled and abundantly pseudocyphellate; hymenium 99–124μ thick, subhymenial layers 35–56μ thick. Spores 8, ellipsoid, 15–20$\times$7–12μ, the spore wall about 1.5μ thick. Pycnidia large, marginal, unstalked; conidia about 1.5$\times$6.0μ, rod-shaped, the ends often somewhat inflated.

MEDULLARY REACTIONS.—K−, C−, KC− or KC+ pinkish, P−, UV−.

CONSTITUENTS.—Imbricaric acid and atranorin.

DISTRIBUTION (Map, Figure 19).—The high mountains of Szechwan and Yunnan, China, and Nepal; on the trunks and stems of trees and shrubs.

Cetrelia collata might be mistaken for *C. davidiana*, *C. delavayana*, *C. nuda*, or *C. sanguinea*. It differs from all these species, however, in producing imbricaric acid rather than some other substance in the medulla. It can easily be distinguished by its C− medullary reaction from *C. davidiana* (with olivetoric acid) and *C. sanguinea* (with anziaic acid), both of which are C+ pink or red in the medulla. From *C. nuda* (with alectoronic and α-collatolic acid) and *C. delavayana* (with perla-



FIGURES 15–21. Distributions. 15. *Cetrelia sanguinea* (Schaer.) Culb. & Culb. 16. *C. japonica* (Zahlbr.) Culb. & Culb. 17. *C. nuda* (Hue) Culb. & Culb. 18. *C. sinensis* Culb. & Culb. 19. *C. collata* (Nyl.) Culb. & Culb. 20. *C. davidiana* Culb. & Culb. 21. *C. delavayana* Culb. & Culb.

tolic acid) it is best distinguished by the appropriate microchemical tests.

CHEMICAL ANALYSIS.—All 17 samples tested contained imbricaric acid and the residue from extracts gave straight needles of oblique extinction in the GE and GAW solutions. Atranorin was easily identified by microcrystal tests. Most extracts were chromatographed before and after base hydrolysis. The hydrolyzed residues frequently showed an additional weak spot at an R_f corresponding to olivetol-2-carboxylic acid and most samples tested showed a definite KC+ pink reaction apparently due to the presence of at least one unidentified substance.

ADDITIONAL SPECIMENS EXAMINED:

CHINA: SZECHWAN: Mt. Lose-chan, south of Ningyüen, 3,950 m., *Handel-Mazzetti* 1441 (WU).

YUNNAN: Lidjiang, Mt. Ndaza Ko, 4,000 m., *Rock*, as *Zahlbr.*, *Lich. Rar. Exs.* 322 (S, UPS, W); Snow Range, 4,300–12,000 ft., *Rock*, 1931 (W); Mt. Yülung-schan, *Handel-Mazzetti* 4254 (WU); between Dali (Talifu) and Hodjing, above Hsiang-schuiho, 26°10′N, 3,400 m., *Handel-Mazzetti* 7398 (*pro parte*) (W); Lopin-chan Pass, above Lan-Kong, *Delavay*, 1888 (PC, 2 collections); Mt. Tsang-chan, above Tali, 400 m., *Delavay*, 1885 (PC), 4,000 m., *Delavay*, 1885 (PC, 2 collections), *Delavay*, 1887 (PC); Fang-Yang-Tschang, above Mo-so-yn, *Delavay*, 1887 (WU); Koua-la-po, 3,000 m., *Delavay*, 1885 (H-Herb. Nylander, PC).

NEPAL: Above Sauwala Khola, 10,500 ft., *Stainton et al.* 4379b (*pro parte*) (BM).

6. Cetrelia davidiana Culb. & Culb., sp. nov. PLATE 16

Thallus mediocris, 9–14 cm. latus; laciniae 0.7–2.2 cm. latae. Superficies superior sordide citrella (albida apud plantas vivas?), levis, pseudocyphellata, pseudocyphellis parvis, ca. 0.5 mm. crassis vel confluentibus et ad 1 mm. Superficies inferior picea, marginibus castanea vel pallida, levis vel subrugosa, fere punctata. Cortex superior 19–31μ crassus, medulla 115–226μ crassa; cortex inferior 12–22μ crassus. Apothecia 0.5–2.0 cm. lata, perforata, primum cupuliformia deinde expansa et radiatofissa, excipulo thallino rugoso et pseudocyphellatissimo; hymenium 71–115μ crassum; subhymenium hyalinum vel subluteum, 40–81μ crassum, stratum crassum algarum tegens. Sporae 8-nae, ellipsoideae, 14–19$\times$7–11μ. Pycnidia numerosa, marginalia, raro in superficie superiore ad margines laciniarum; conidia 1$\times$3–5μ recta, extremis nonnihil inflatis.

Thallus medium, 9–14 cm. broad; lobes 0.7–2.2 cm. broad. Upper surface uniformly light tan (whitish when fresh?), smooth, pseudocyphellate, the pores small, about 0.5 mm. in diameter, or becoming confluent and reaching 1 mm. Lower surface jet-black, the margins brown or colored like the upper surface, smooth or somewhat wrinkled, especially at the ascendent margins of the lobes, if punctate, the puncta restricted to the crests of the ridges. Upper cortex 19–31μ thick;

medulla 115–226μ thick; lower cortex 12–22μ thick. Apothecia 0.5–2.0 cm. in diameter, perforate, cup-shaped at first then expanded and split longitudinally, the thalloid exciple much wrinkled and abundantly pseudocyphellate; hymenium 71–115μ thick; subhymenial layers colorless or pale yellowish, 40–81μ thick, immediately underlain by a thick zone of algae. Spores 8, ellipsoid, 14–19$\times$7–11μ, the spore wall relatively thick, 1.0–1.7μ. Pycnidia abundant, marginal or a few laminal toward the margin of the lobes; conidia 1$\times$3–5μ, rod-shaped, the ends of some somewhat enlarged.

TYPE.—"In montis Yülung-schan prope urbem Lidjiang ["Likiang"], Yunnan," China, *Handel-Mazzetti* 4254 (W, holotype).

MEDULLARY REACTIONS.—K−, C+ pink, PD−.

CONSTITUENTS.—Olivetoric acid and atranorin.

DISTRIBUTION (Map, Figure 20).—Mountains of Szechwan and Yunnan, China; on the bark of trees.

Cetrelia davidiana is a Chinese species without soredia, isidia, or lobulae. It is similar to *C. olivetorum* chemically and in that it has minute pseudocyphellae, but differs in that it is esorediate. It is also similar to *C. pseudolivetorum* but differs in that it lacks the marginal lobulae.

Cetrelia davidiana must be distinguished chemically from similar esorediate and nonisidiate species most closely related to it. The positive reaction of the medulla with C will suffice to separate it from *C. collata* and *C. nuda* and even from *C. alaskana* and *C. delavayana*, the latter two of which also differ morphologically in possessing small and inconspicuous pseudocyphellae rather than large and obvious ones. The medullary reaction of *C. davidiana* with C is generally a pink or rose due to the presence of olivetoric acid while that of *C. sanguinea*, containing anziaic acid, is usually bright red. But definitive microchemical tests are obviously preferable here to the thallus spot tests.

CHEMICAL ANALYSIS.—The extracts from fragments of seven samples were tested. Atranorin was usually determined by crystals in the GE and GA*o*-T solution and by chromatography. Olivetoric acid was crystallized from the GE, GAW, and GA*o*-T solutions and was confirmed by chromatography to distinguish it definitely from anziaic acid. Physodic acid did not occur with olivetoric acid in any of the samples tested.

SPECIMENS EXAMINED:

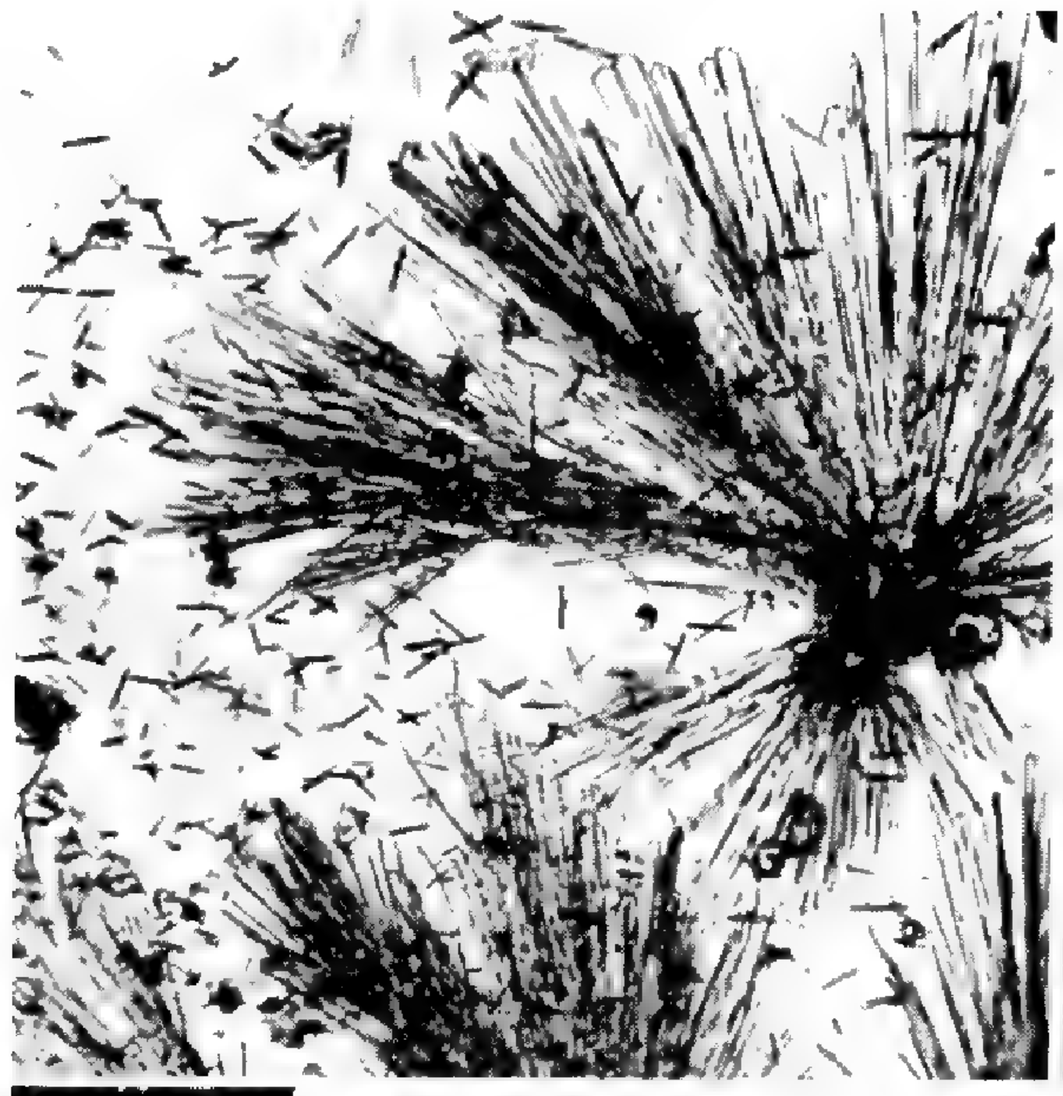
CHINA: SZECHWAN: Above Fumadi, Wolo-ho River between Yenyüen and Yungning, ca. 3,300 m., *Handel-Mazzetti* 3039 (WU).

YUNNAN: Between Dali (Talifu) and Hodjing, above Hsiang-schuiho, 26°15′N, ca. 3,400 m., *Handel-Mazzetti* 7398 (*pro parte*) (W, 2 collections); Mt. Yülung-schan near Lidjiang, *Handel-Mazzetti* 4254 (W, WU); Ti-ou-ze Pass, above Ta-pin-tze, *Delavay*, 1888 (PC); Koua-la-po (Ho Kin), 3,000 m., *Delavay*, 1885 (PC).

PLATES

PLATE 1

Crystals produced by substances in the microcrystal-test solutions: 1. Alectoronic acid and α-collatolic acid cocrystallized in GE. The smaller crystals are atranorin. Prepared from the acetone extract after benzene extraction of *Cetrelia chicitae* (×125). 2. Alectoronic acid and α-collatolic acid cocrystallized in GE. Prepared from the acetone extract after benzene extraction of *Cetrelia braunsiana* (×110). 3. Alectoronic acid and α-collatolic acid cocrystallized in GAW. Prepared from the acetone extract after benzene extraction of *Cetrelia chicitae* (×200). 4. Anziaic acid recrystallized in GE. Prepared from the acetone extract after benzene extraction of *Cetrelia isidiata* (×450). 5. Anziaic acid recrystallized in GAW. Prepared from the acetone extract after benzene extraction of *Cetrelia isidiata* (×165). 6. Atranorin recrystallized in GE. Prepared from the acetone extract after benzene extraction of *Cetrelia sanguinea* (×140).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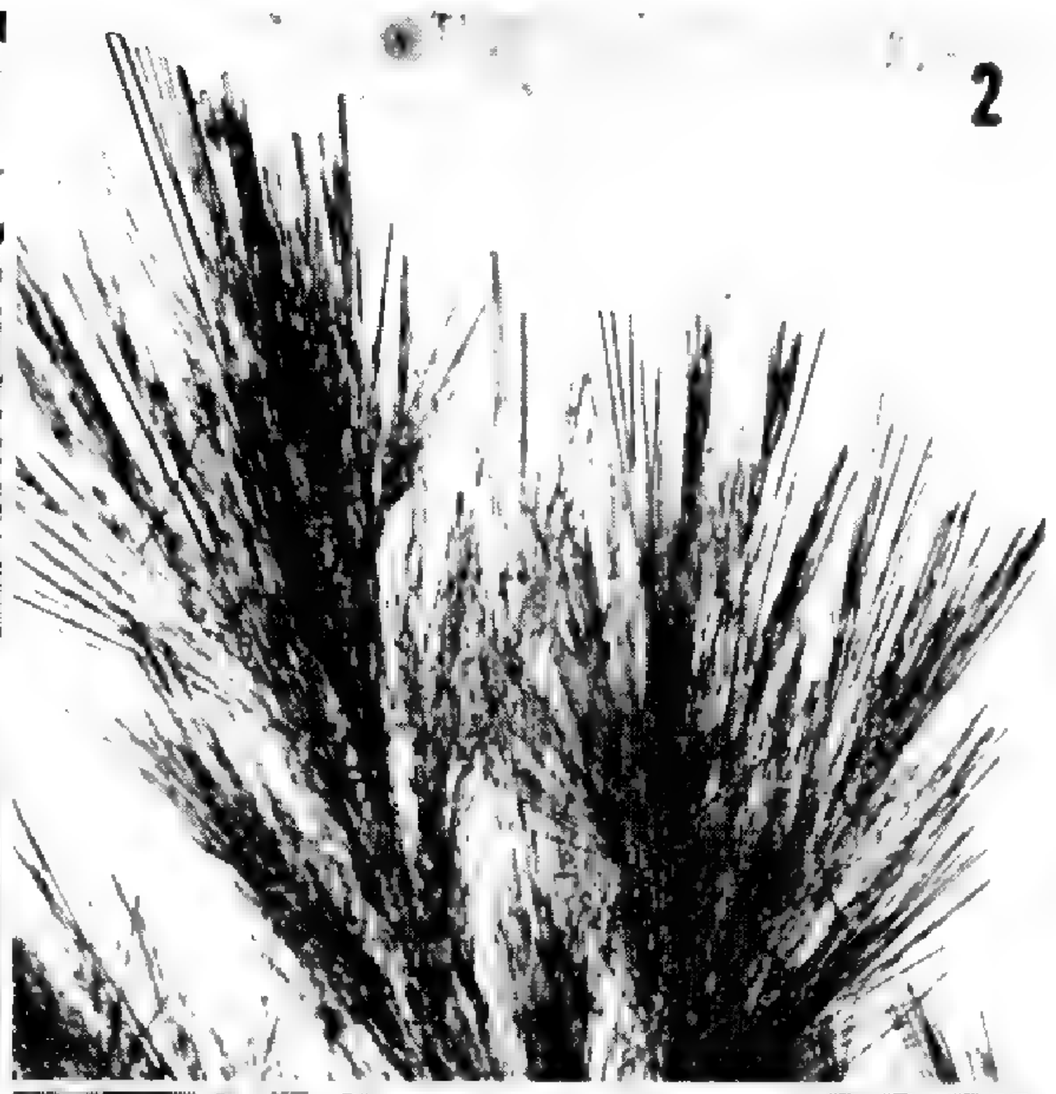
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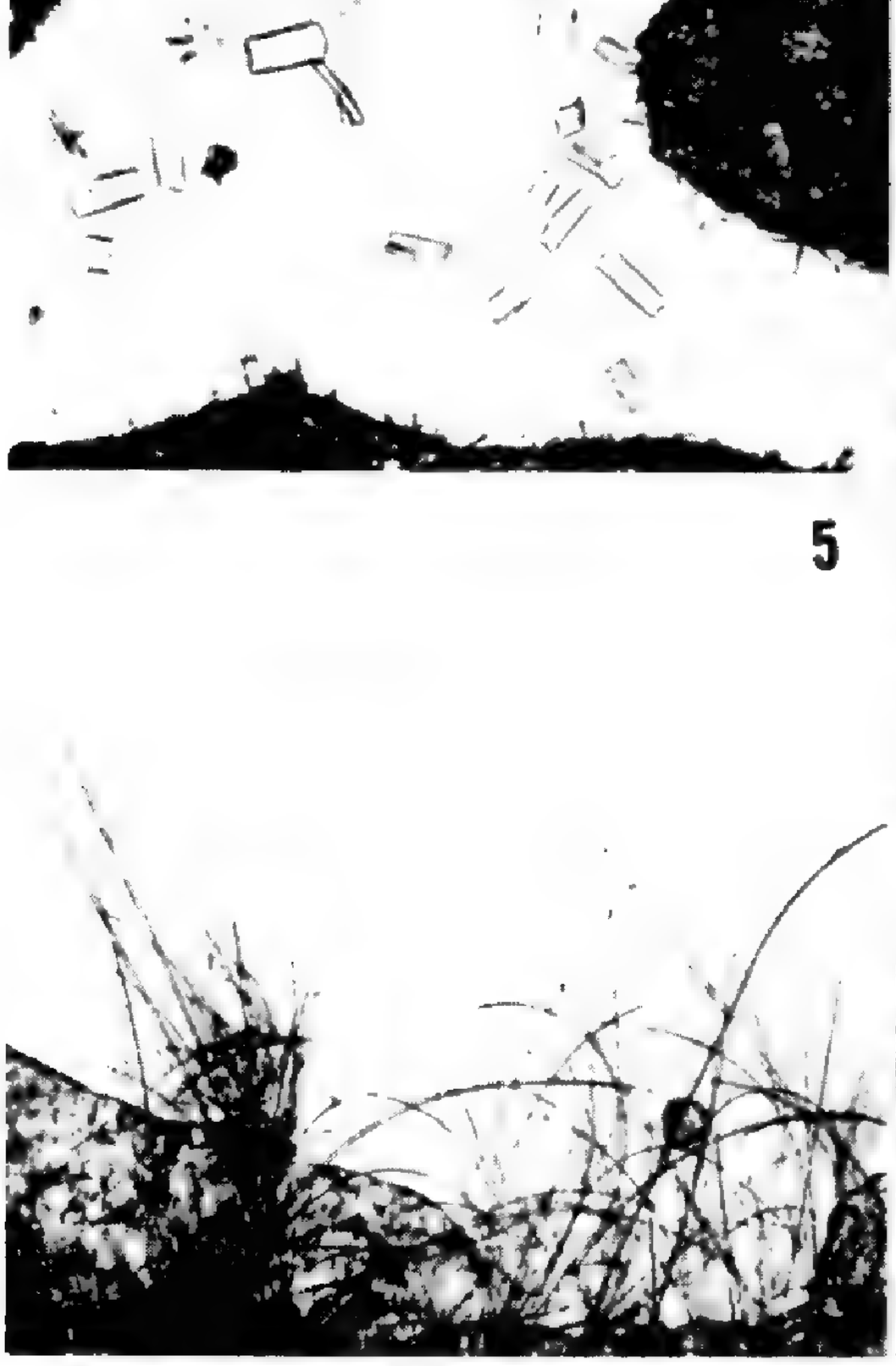
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PLATE 2

Crystals produced by substances in the microcrystal-test solutions: 7. The yellow atranorin condensation product with GA*o*-T. Prepared from the benzene extract of *Platismatia erosa* (×120). 8. The yellow atranorin condensation product with *o*-toluidine in GA*o*-T. Prepared from the benzene extract of *Platismatia tuckermanii* (×110). 9. The yellow atranorin condensation product with *o*-toluidine in GA*o*-T showing two crystal types, the larger needles typical of the atranorin derivative. The smaller, more densely clustered needles may be due to an unidentified substance. Prepared from the benzene extract of *Platismatia interrupta* (×130). 10. Yellow crystals of the condensation product of atranorin and *o*-toluidine in GA*o*-T distorted by the accompanying colorless caperatic acid. Prepared from the acetone extract after benzene extraction of *Platismatia tuckermanii* (×135). 11. Caperatic acid recrystallized in GAW. Prepared from the acetone extract of benzene-extracted *Platismatia erosa* (×115). 12. Caperatic acid recrystallized in GAW showing typical crystals and abnormal curly plates toward the center of the clusters. Prepared from the acetone extract of benzene-extracted *Platismatia interrupta* (×100).

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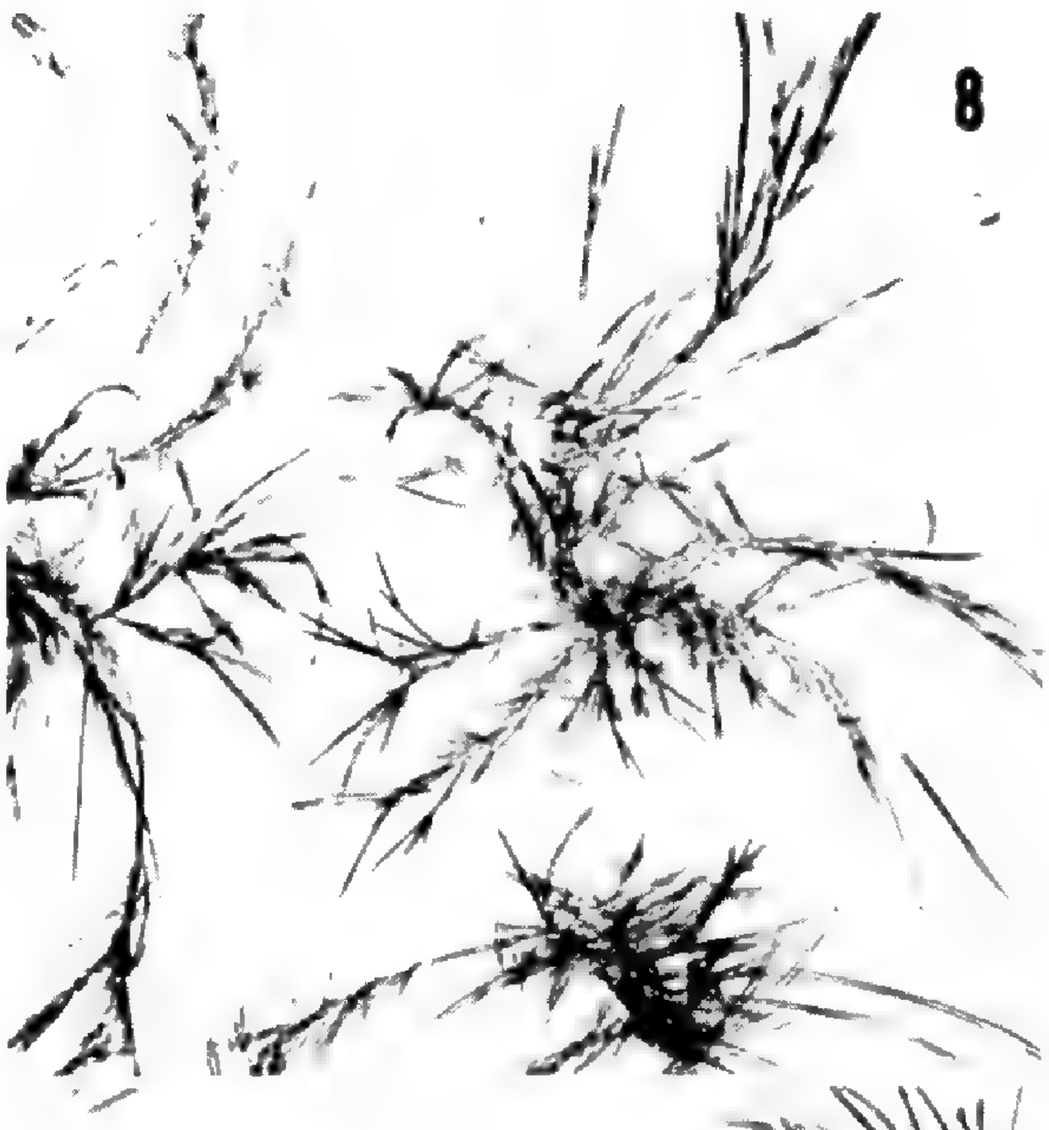
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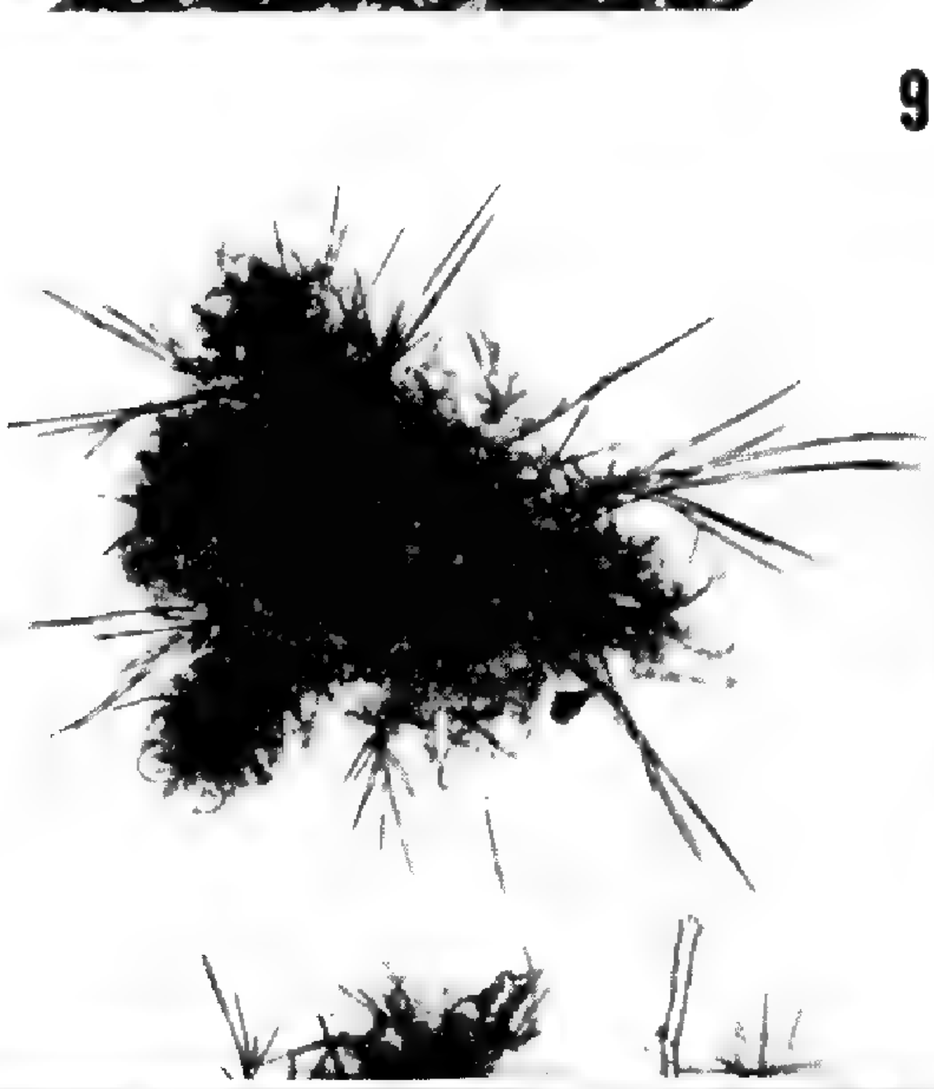
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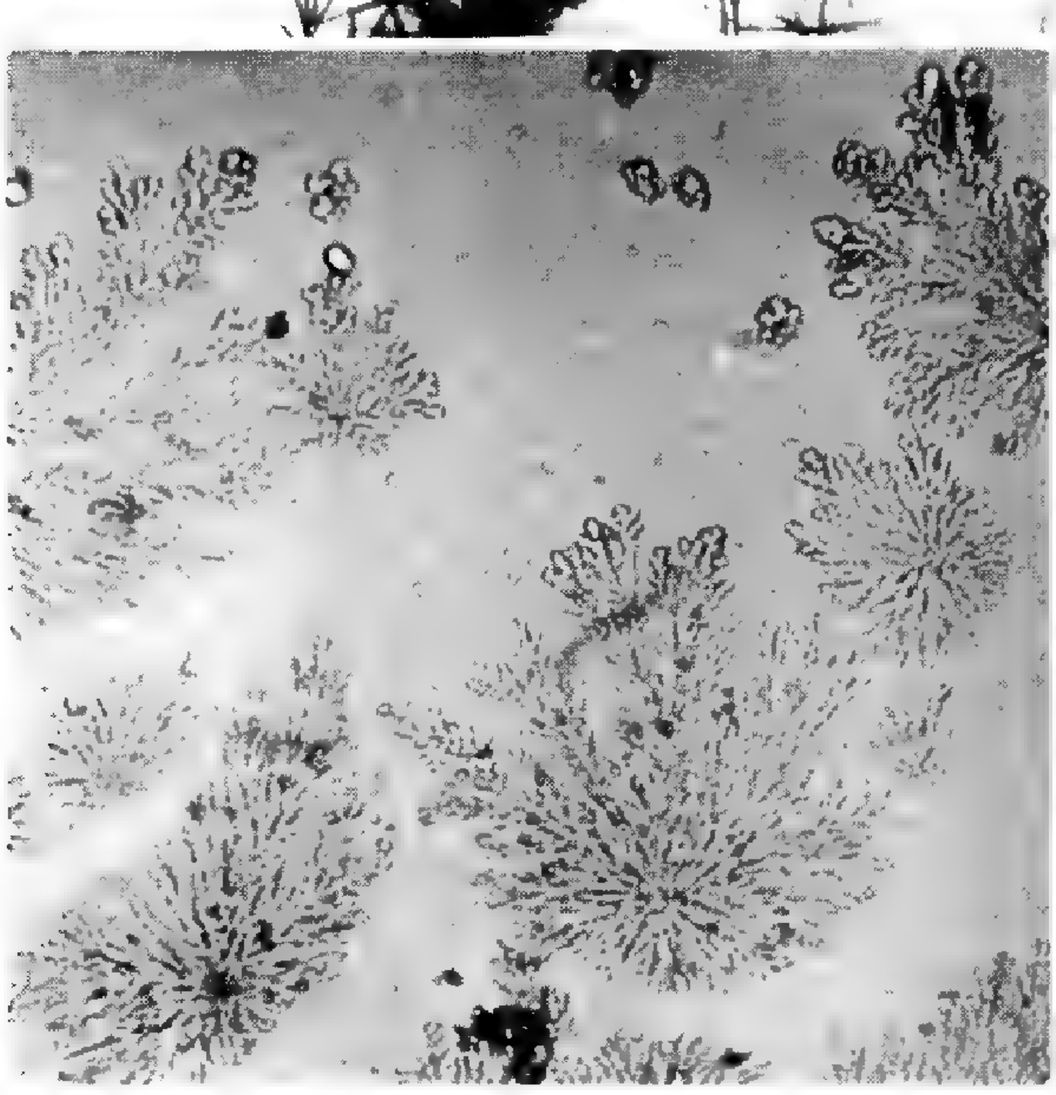
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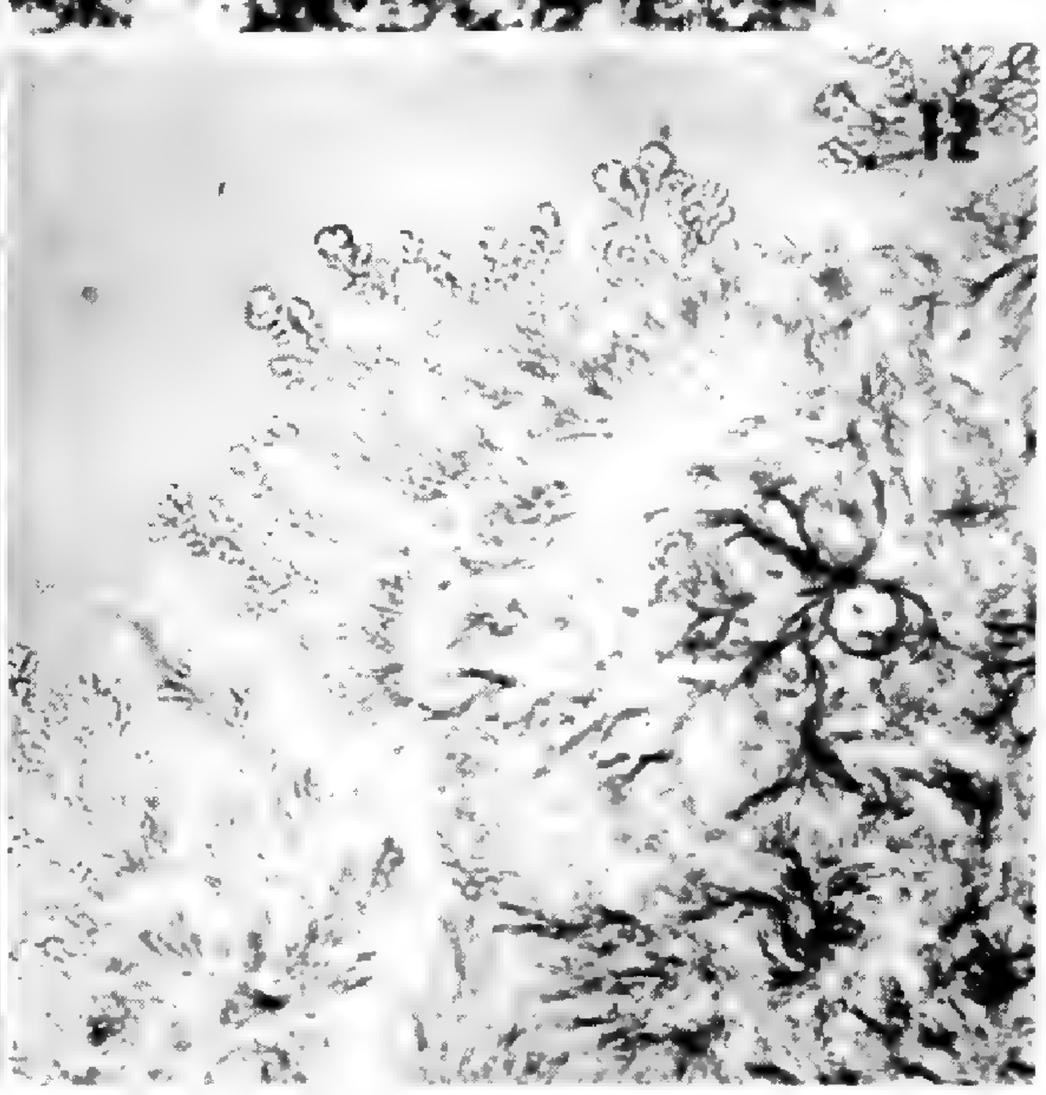
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PLATE 3

Crystals of caperatic acid in the microcrystal-test solutions: 13. The "cloud" form of caperatic acid from recrystallization in GE. Prepared from caperatic acid isolated from *Parmelia cryptochlorophaea* (×240). 14. The "cloud" form of caperatic acid from recrystallization in GE. Prepared from the acetone extract of benzene-extracted *Platismatia glauca* (×140). 15. The "plate" form of caperatic acid from recrystallization in GE. Prepared from a pure sample of caperatic acid isolated from *Parmelia cryptochlorophaea* (×120). 16. The "plate" form of caperatic acid from recrystallization in GE. Prepared from the acetone extract of benzene-extracted *Platismatia glauca* (×130). 17. Mixed crystal forms of caperatic acid from recrystallization in GE. Prepared from pure caperatic acid isolated from *Parmelia cryptochlorophaea* (×120). 18. Mixed crystal forms of caperatic acid from recrystallization in GE. Needles and prisms of atranorin are also present. Prepared from the acetone extract of benzene-extracted *Platismatia erosa* (×110).

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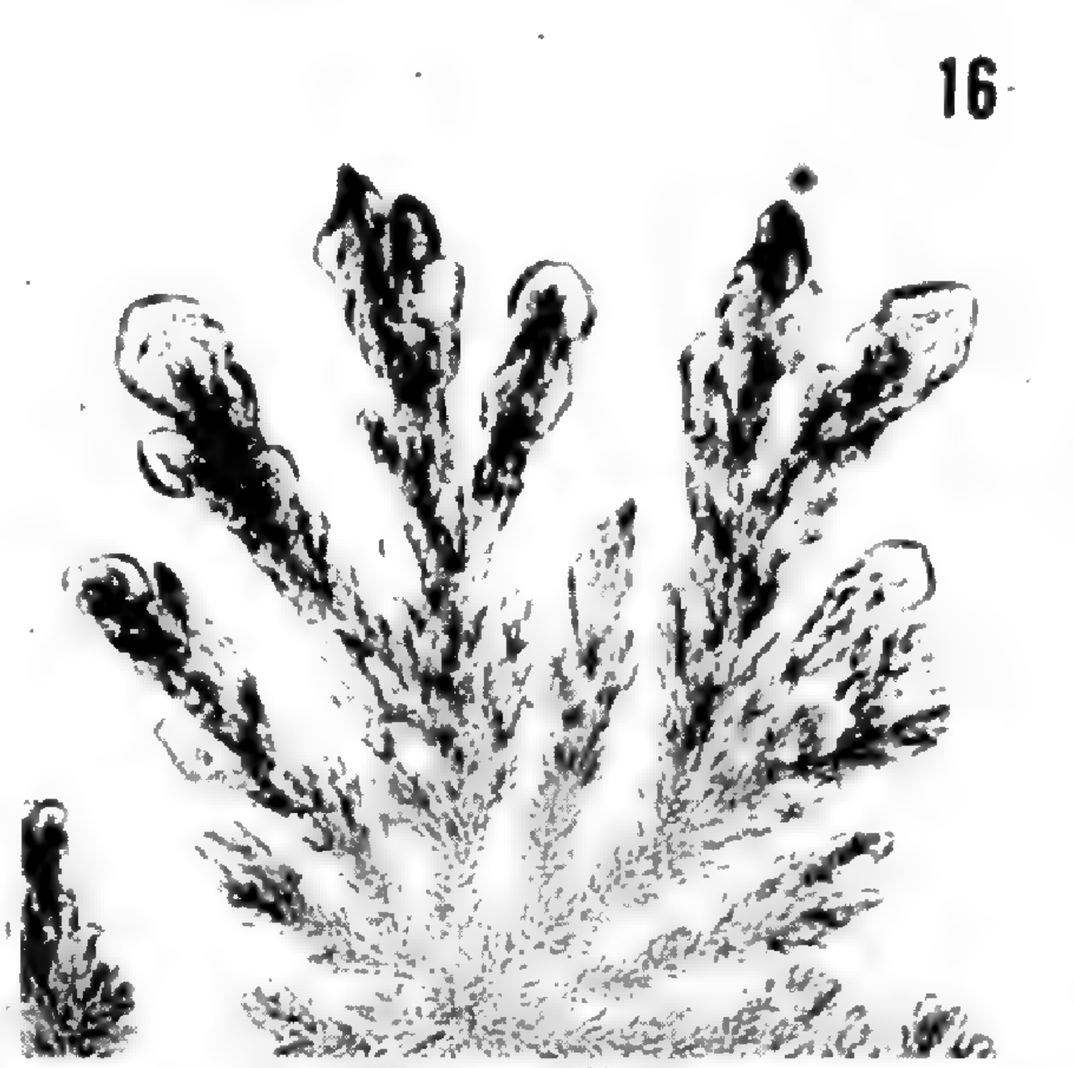
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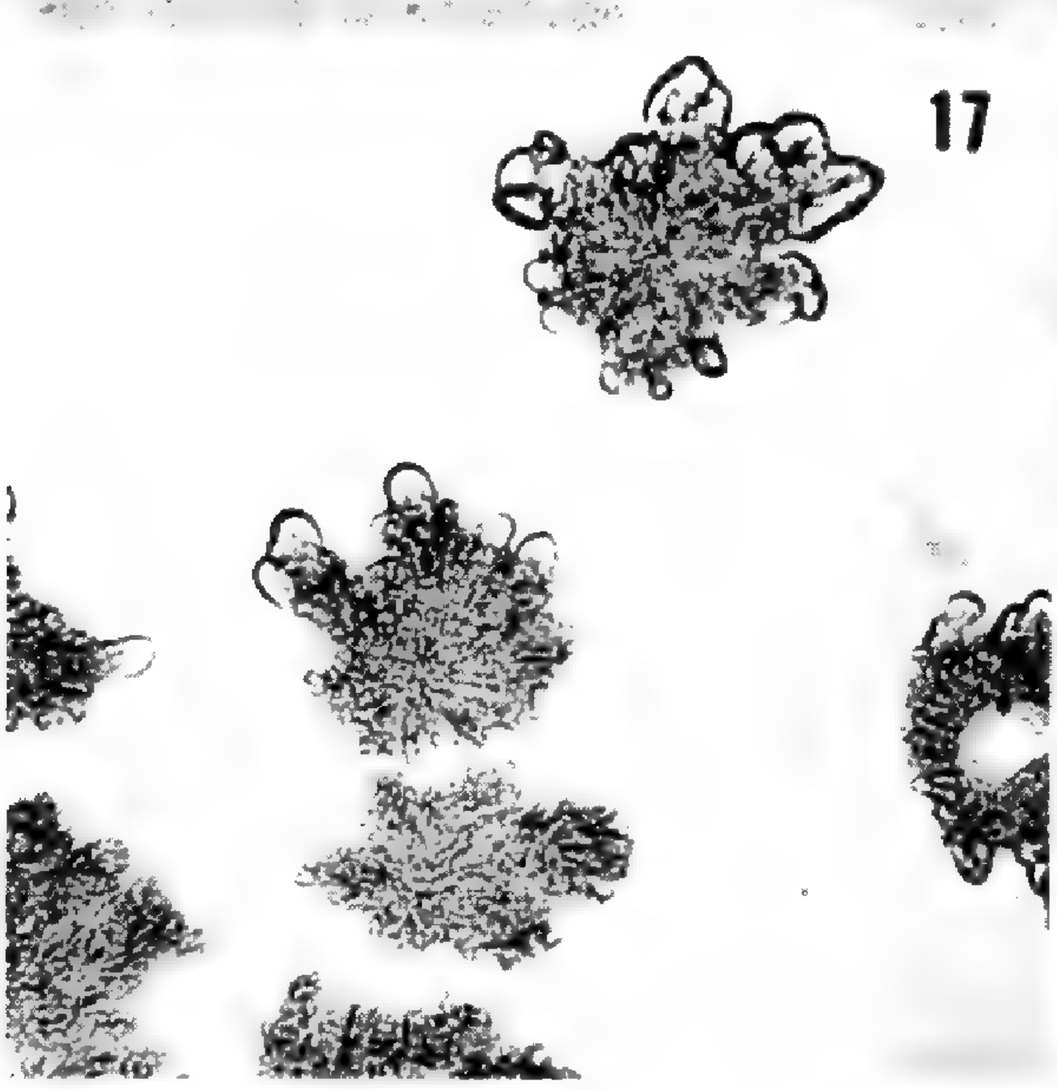
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PLATE 4

Crystals produced by substances in the microcrystal-test solutions: 19. Pure norcaperatic acid recrystallized in GE (×165). 20. Pure norcaperatic acid recrystallized in GAW (×110). 21. Imbricaric acid (large needles) and atranorin (small prisms) recrystallized in GE. Prepared from the benzene extract of *Cetrelia cetrarioides* (×110). 22. Imbricaric acid recrystallized in GAW. Prepared from the benzene extract of *Cetrelia cetrarioides* (×115). 23. The *o*-toluidine salt of imbricaric acid (colorless needles) in GA*o*-T. The fuzzy crystals barely visible are yellow and may be a cocrystallization with the atranorin condensation product with *o*-toluidine. Prepared from the benzene extract of *Cetrelia sinensis* (×130). 24. Small yellow crystals beside the atranorin condensation product with *o*-toluidine in GA*o*-T; commonly observed in samples containing imbricaric acid. Such crystals may be due to cocrystallization or to an unidentified substance. Prepared from the benzene extract of *Cetrelia cetrarioides* containing imbricaric acid (×130).

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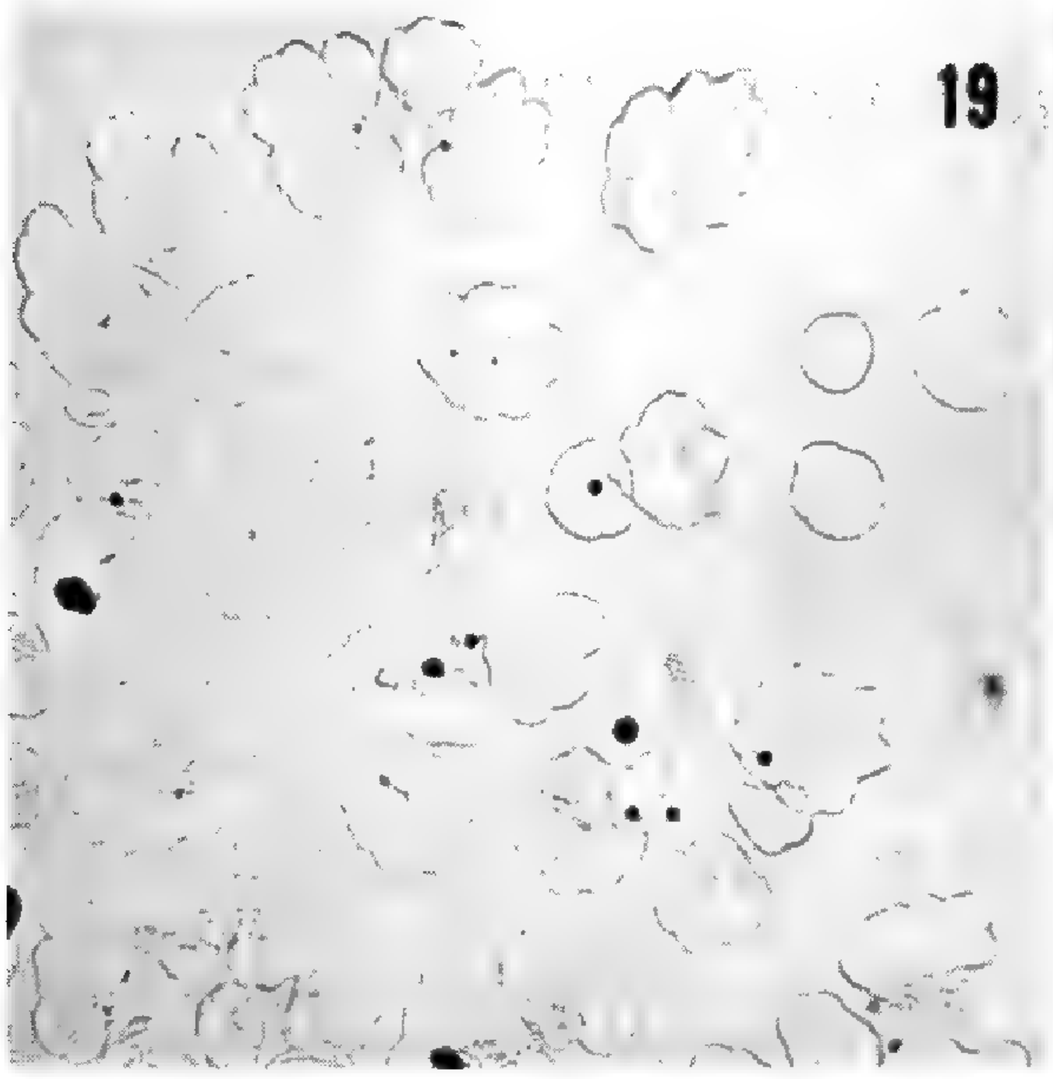

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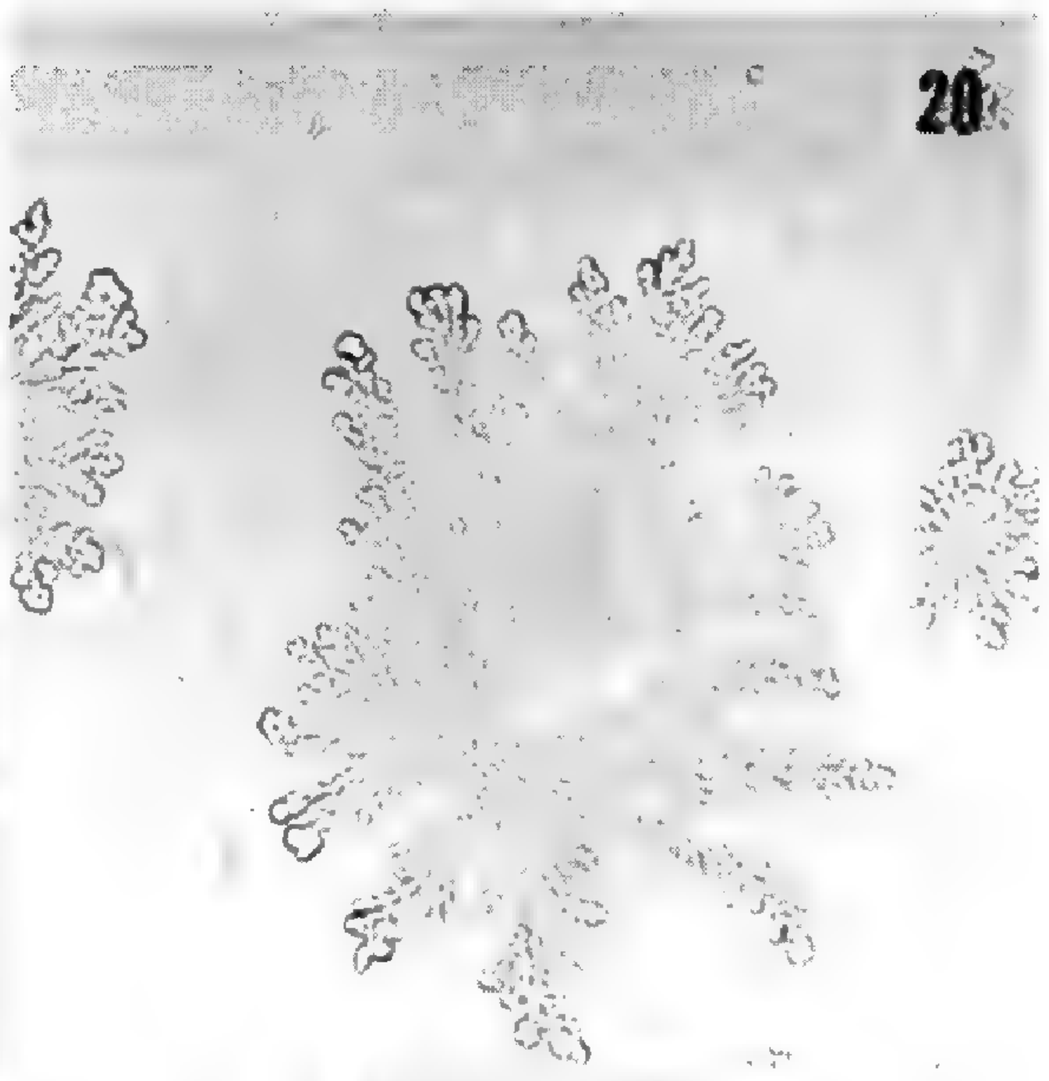

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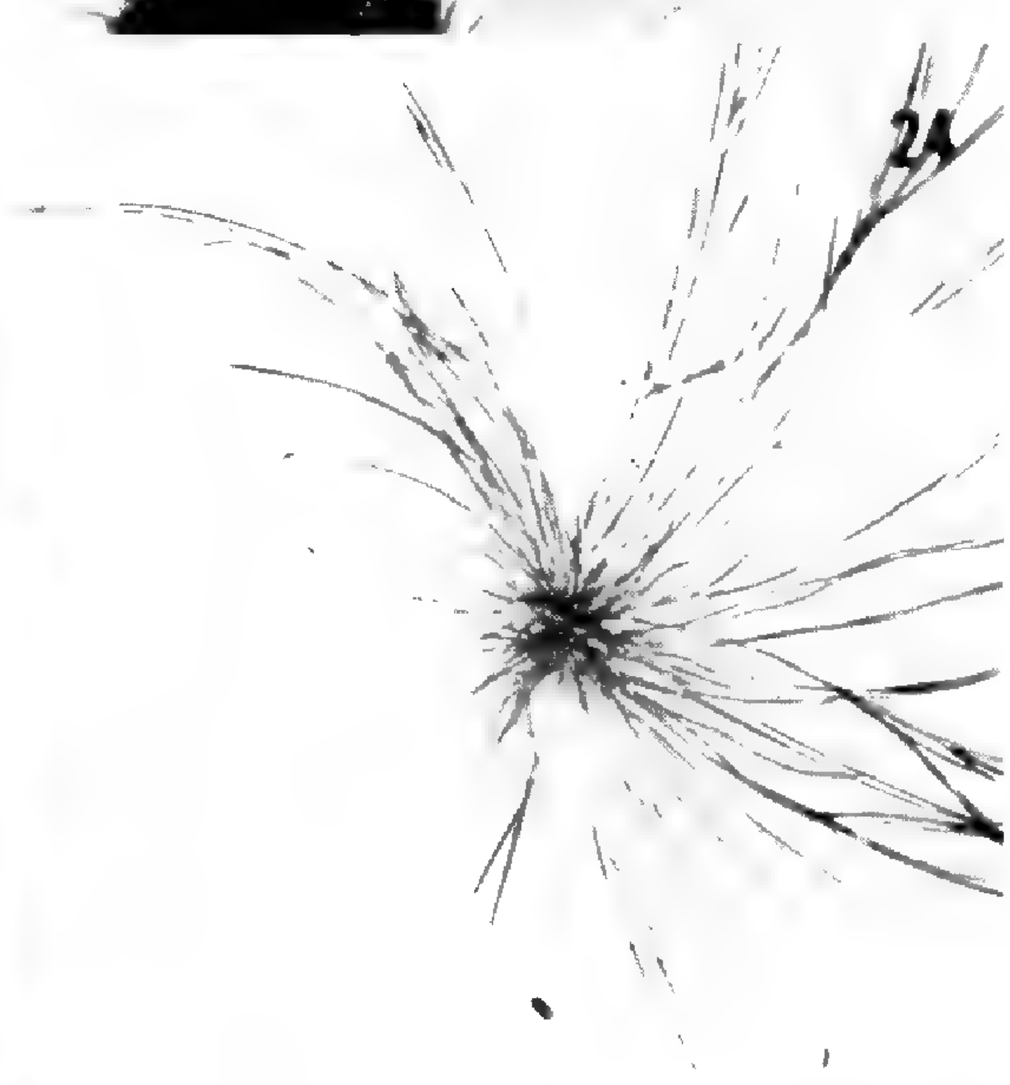

PLATE 5

Crystals produced by substances in the microcrystal-test solutions: 25. Microphyllinic acid recrystallized in GE. Prepared from the benzene extract of *Cetrelia japonica* (×120). 26. Microphyllinic acid recrystallized in GAW. Prepared from the benzene extract of *Cetrelia japonica* (×135). 27. The sodium salt of microphyllinic acid precipitated in 5% aqueous sodium hydroxide. Prepared from the benzene extract of *Cetrelia japonica* (×110). 28. Olivetoric acid recrystallized in GE. Prepared from the acetone extract of benzene-extracted *Cetrelia olivetorum* (×490). 29. Olivetoric acid recrystallized in GAW. Prepared from the acetone extract of benzene-extracted *Cetrelia davidiana* (×120). 30. The colorless *o*-toluidine salt of olivetoric acid in GA*o*-T. Prepared from the acetone extract of benzene-extracted *Cetrelia olivetorum* (×110)

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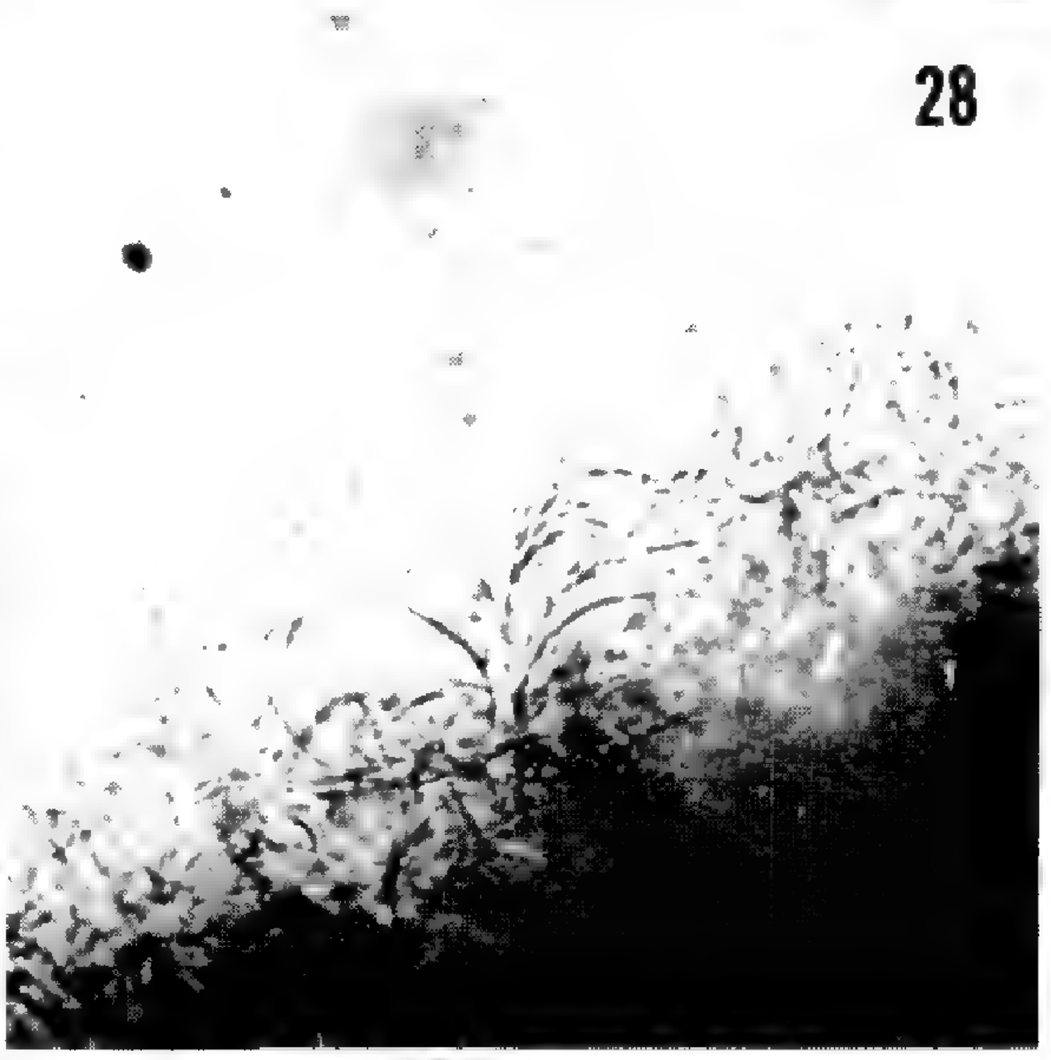
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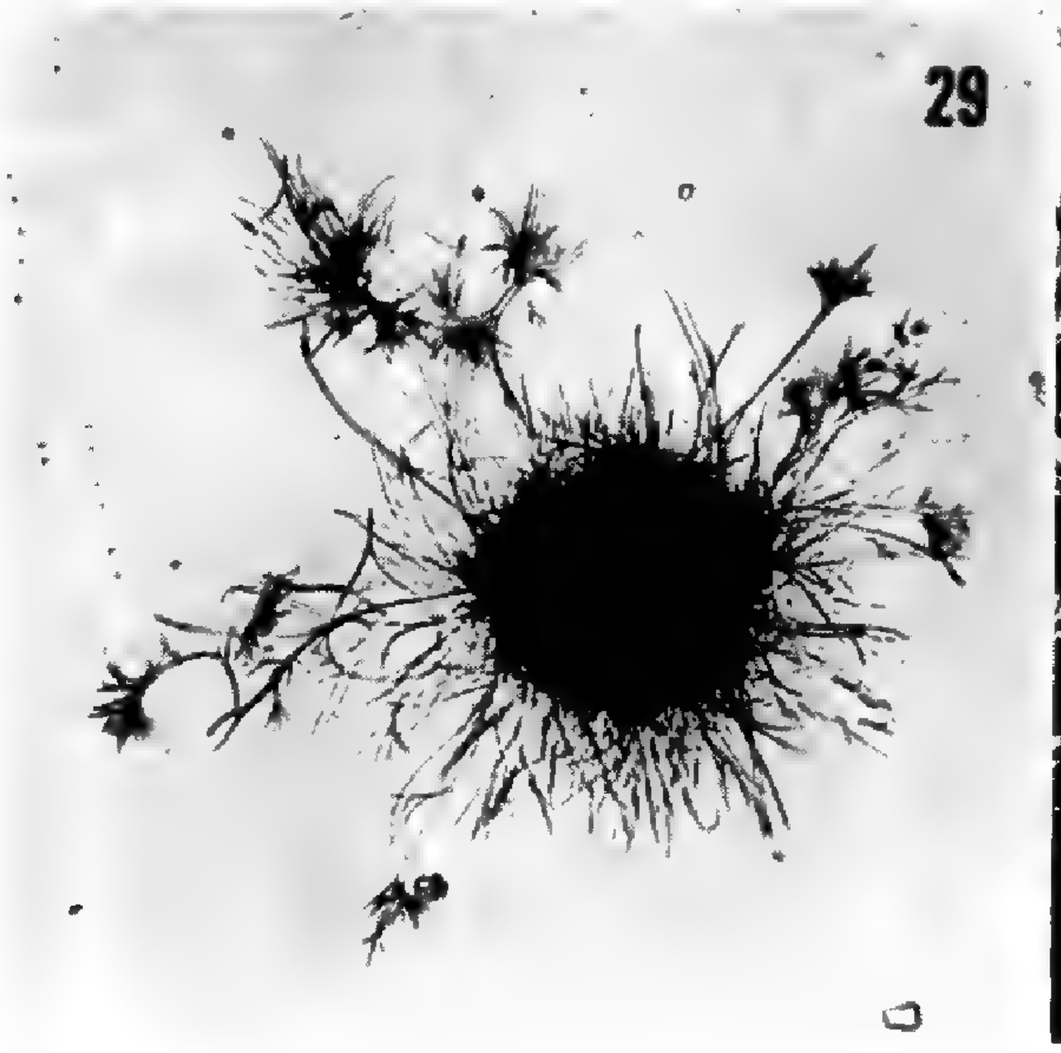
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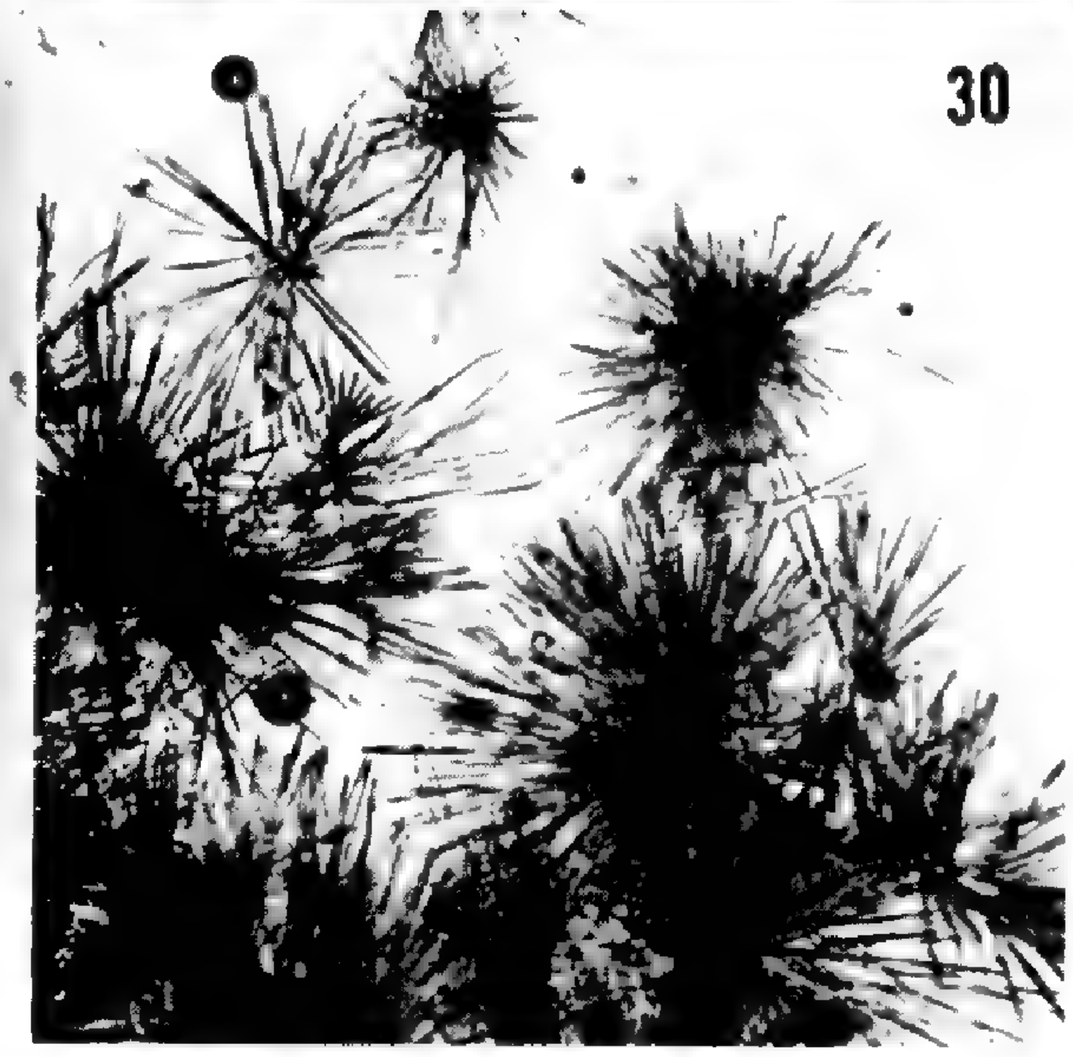
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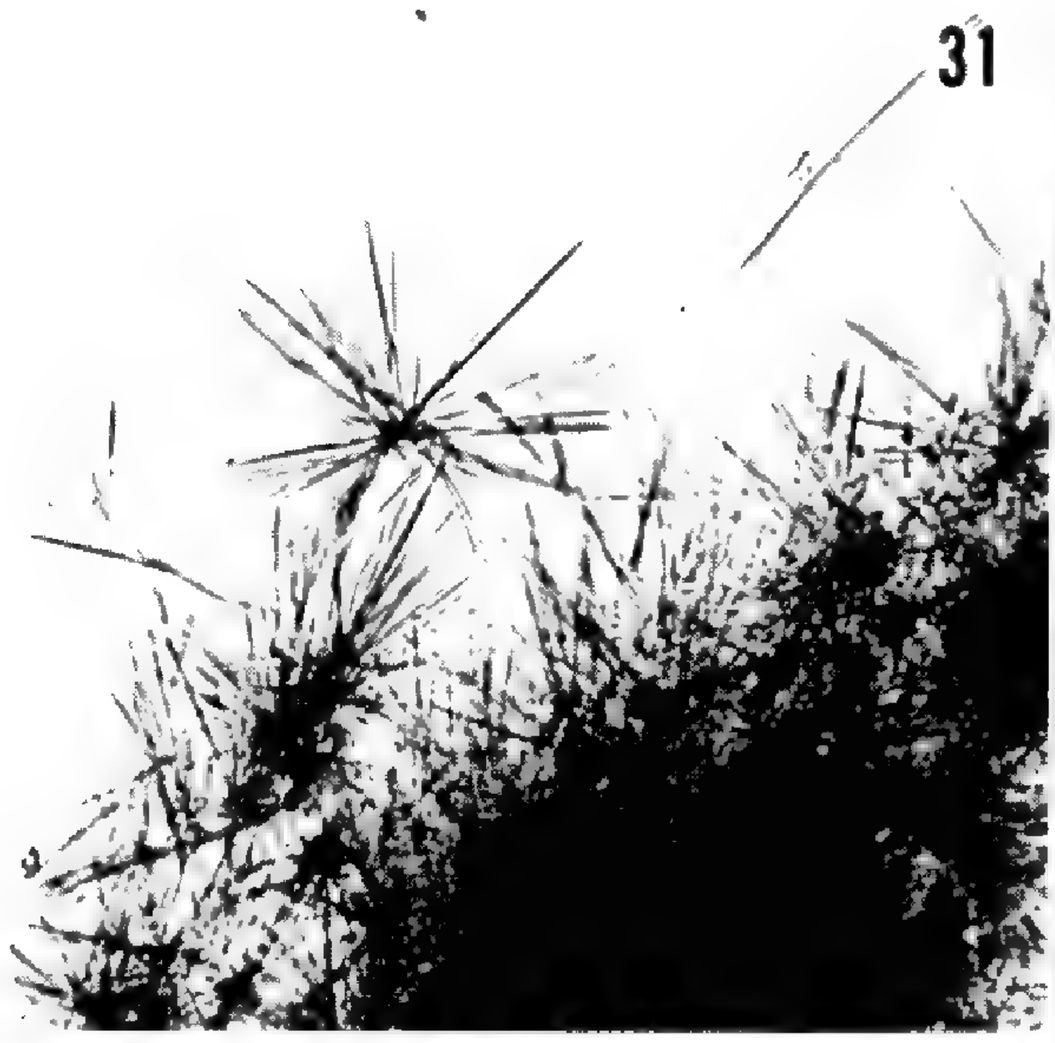
PLATE 6

Crystals produced by substances in the microcrystal-test solutions: 31. The colorless *o*-toluidine salt of olivetoric acid in GA*o*-T. Prepared from the acetone extract of benzene-extracted *Cetrelia pseudolivetorum* (×140). 32. Perlatolic acid recrystallized in GE. Prepared from the benzene extract of *Cetrelia cetrarioides* (×115). 33. Perlatolic acid recrystallized from GAW. Prepared from the benzene extract of *Cetrelia delavayana* (×115). 34. The *o*-toluidine salt of perlatolic acid (large colorless crystals) and atranorin (small yellow clusters) in GA*o*-T. Prepared from the benzene extract of *Cetrelia delavayana* (×170). 35. Yellow crystals of an unidentified substance crystallized in GE. Prepared from an extract of *Platismatia erosa* (×380). 36. Unidentified yellowish-tan crystals formed in GA*o*-T from an extract of *Platismatia interrupta* (×100).

31



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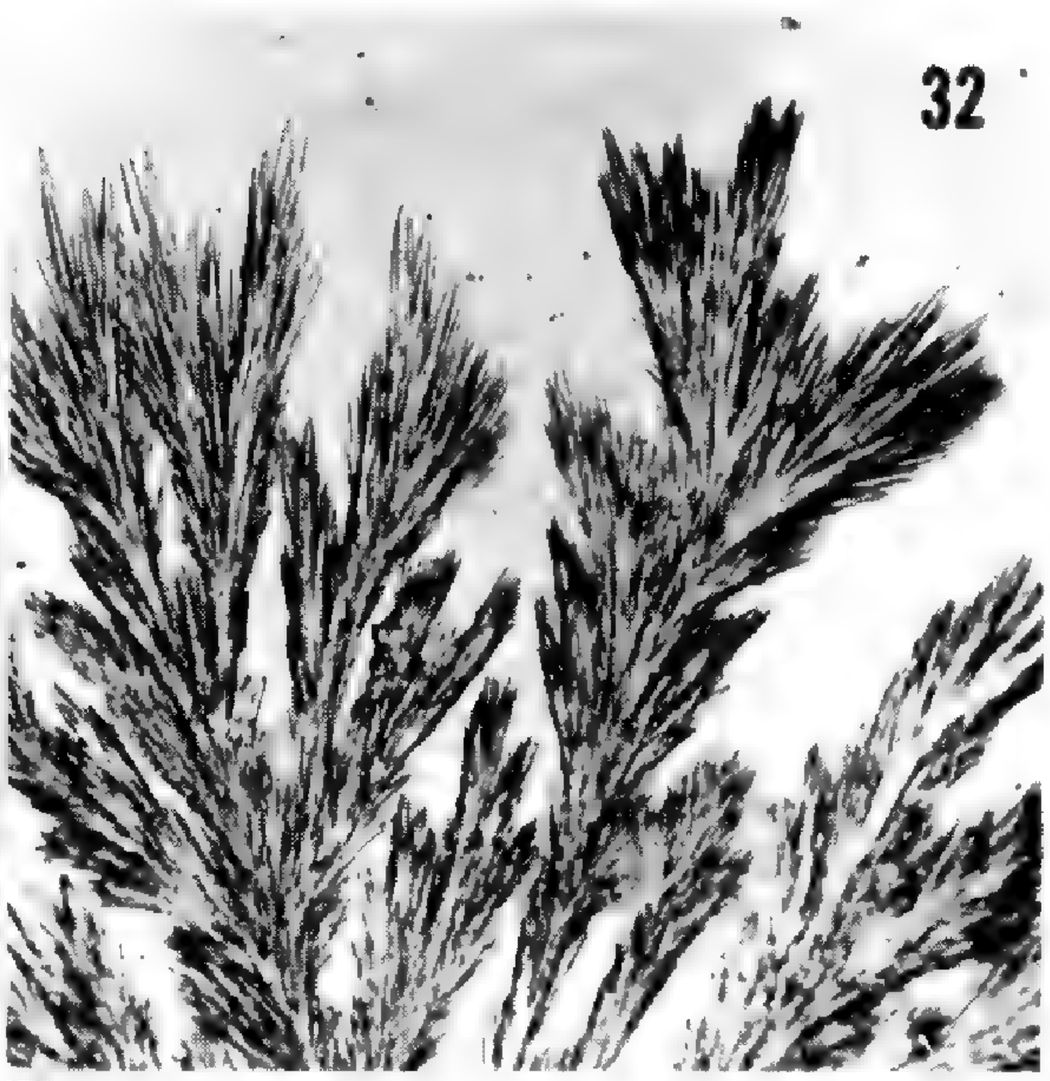

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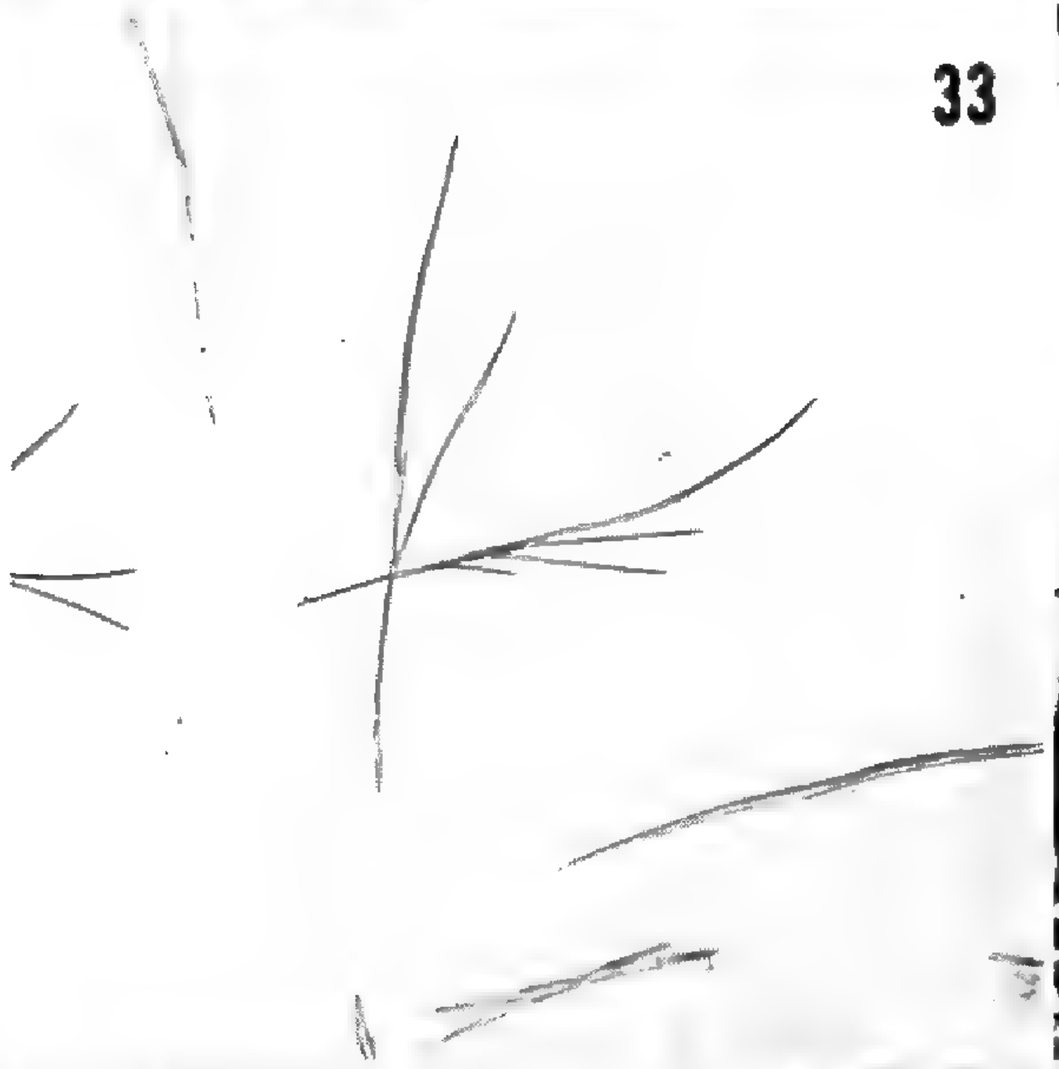

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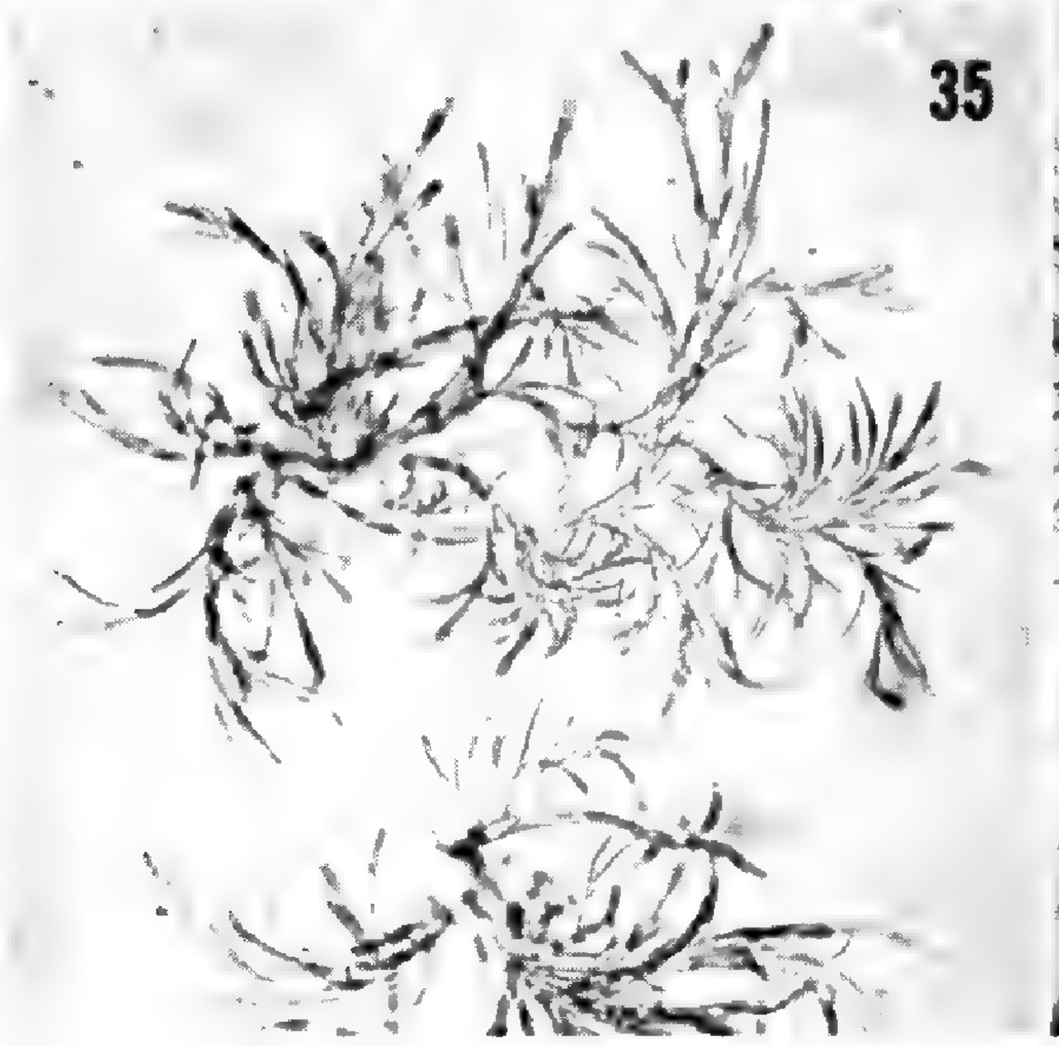

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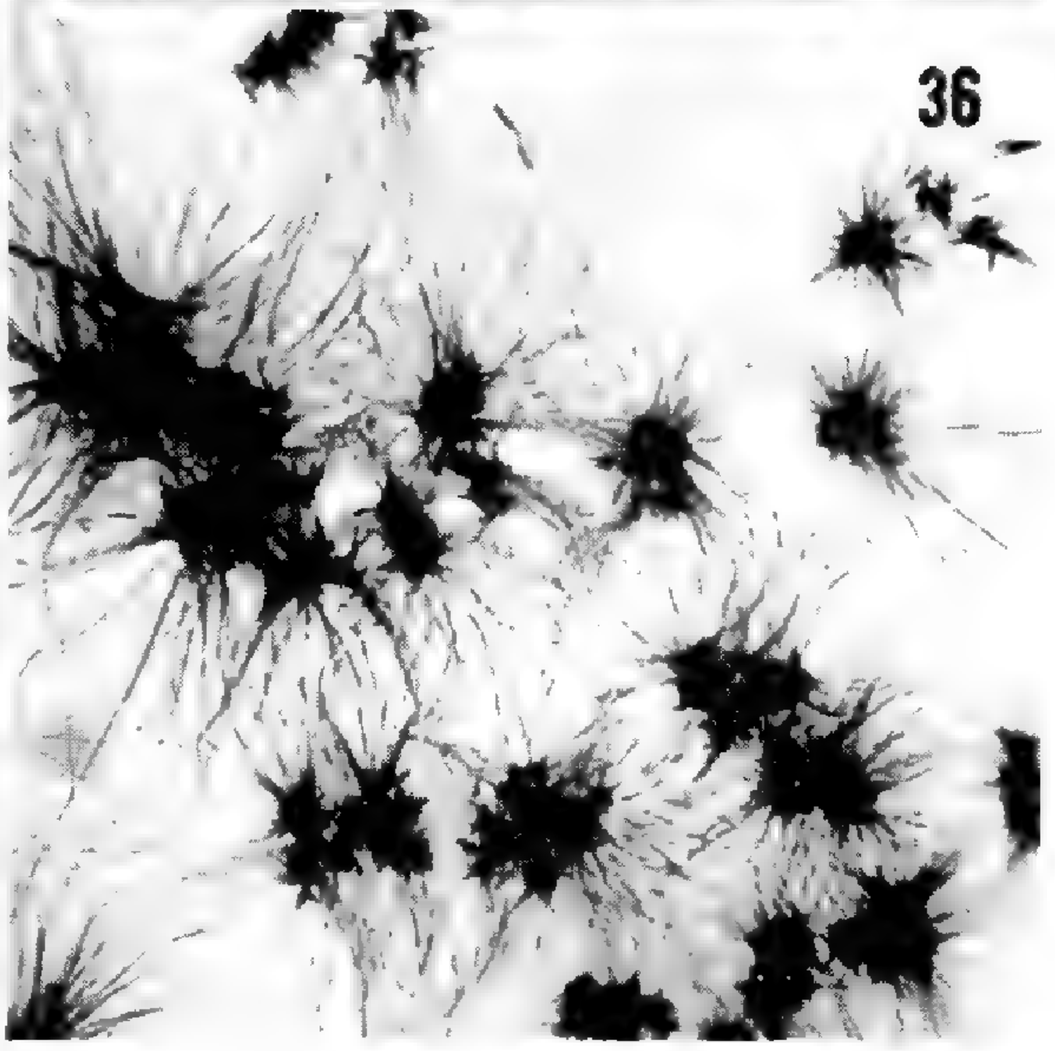

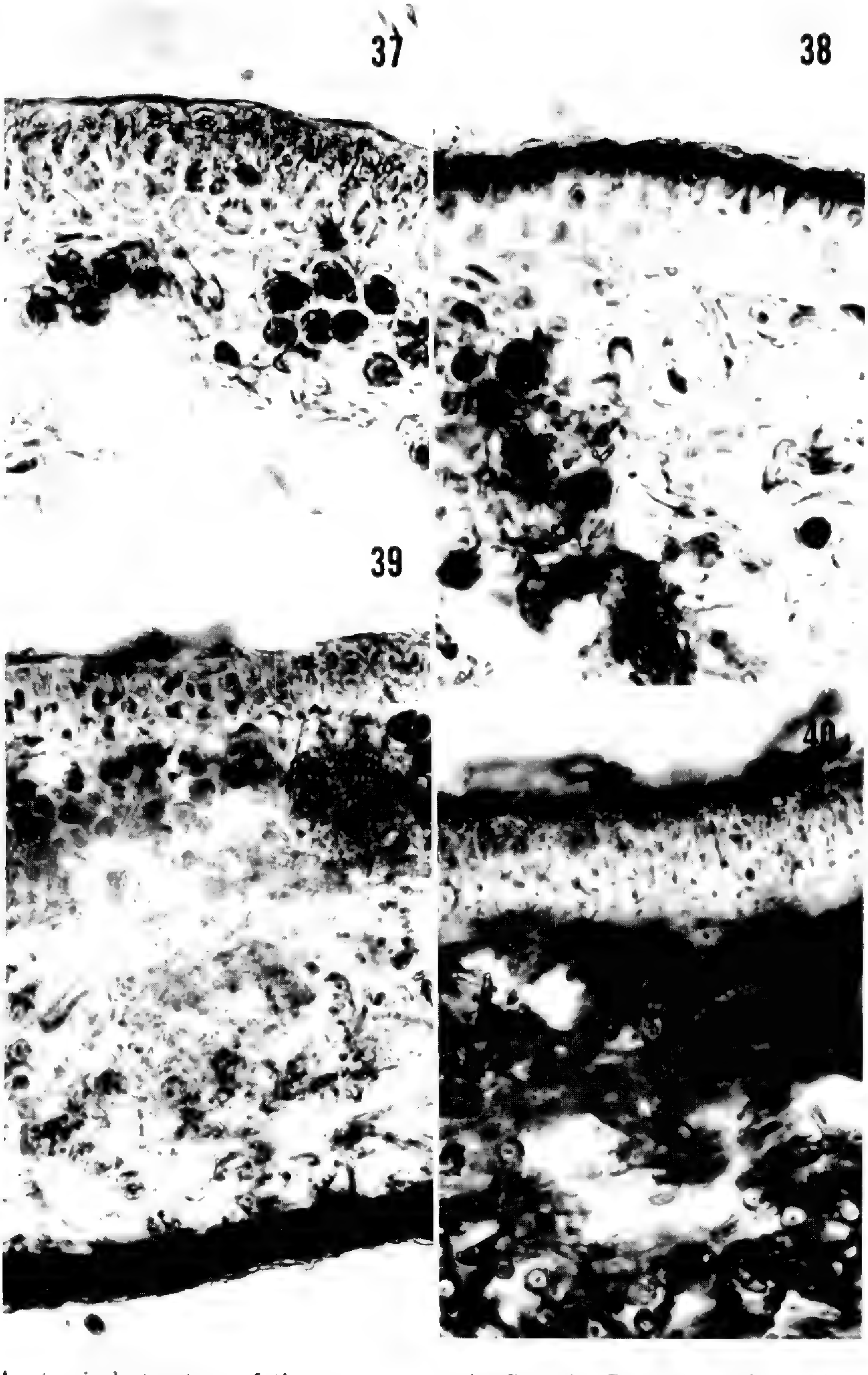

Anatomical structure of the upper cortex in *Cetraria*, *Parmelia*, and *Asahinea*: 37. Paraplectenchymatous cortex of *C. oakesiana* Tuck. 38. Same, *C. ericetorum* Opiz. 39. Prosoplectenchymatous cortex of *P.* (*Amphigymnia*) *stuppea* Tayl. 40. Same, *A. chrysantha* (Tuck.) Culb & Culb. All photographs ×300.

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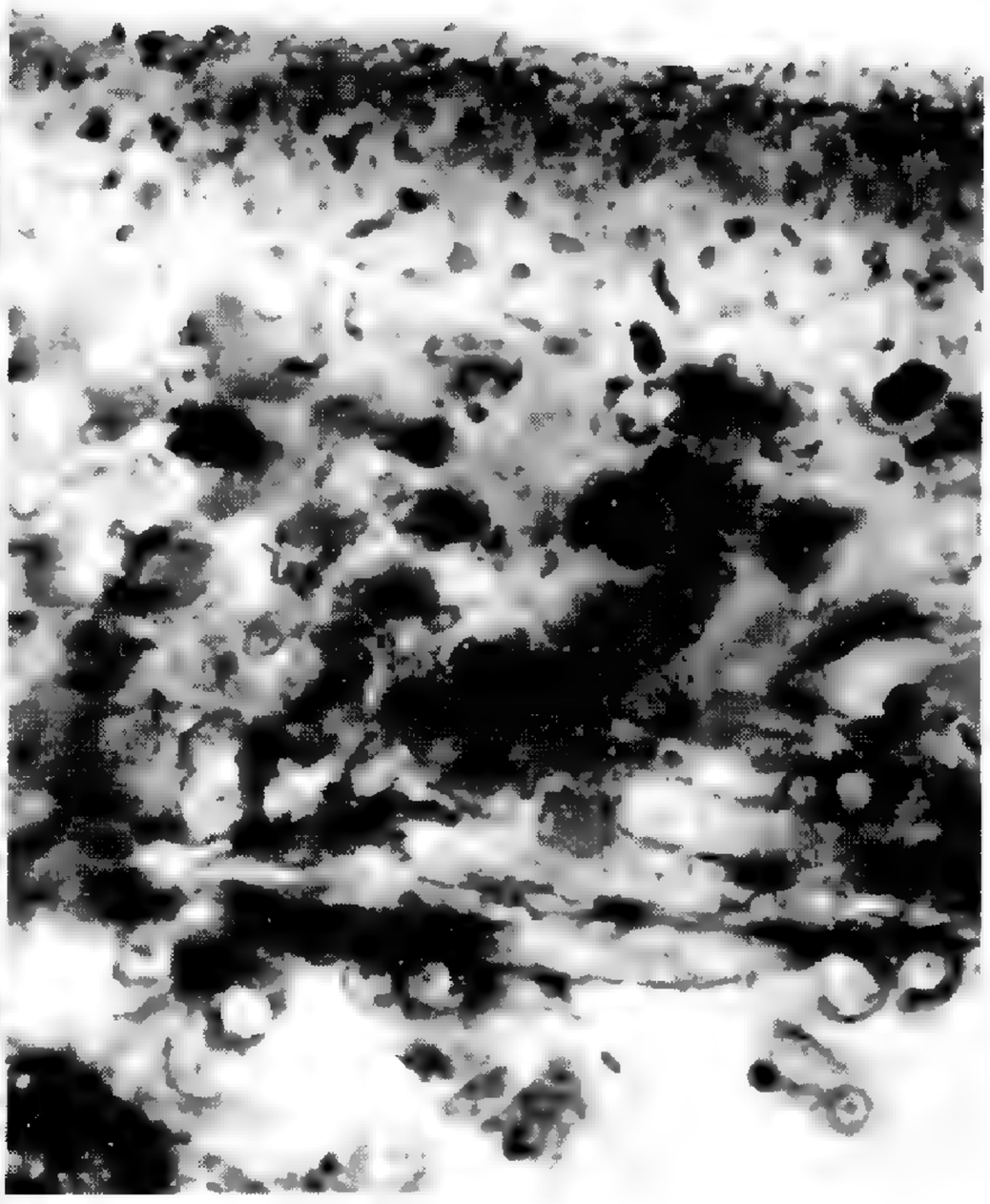

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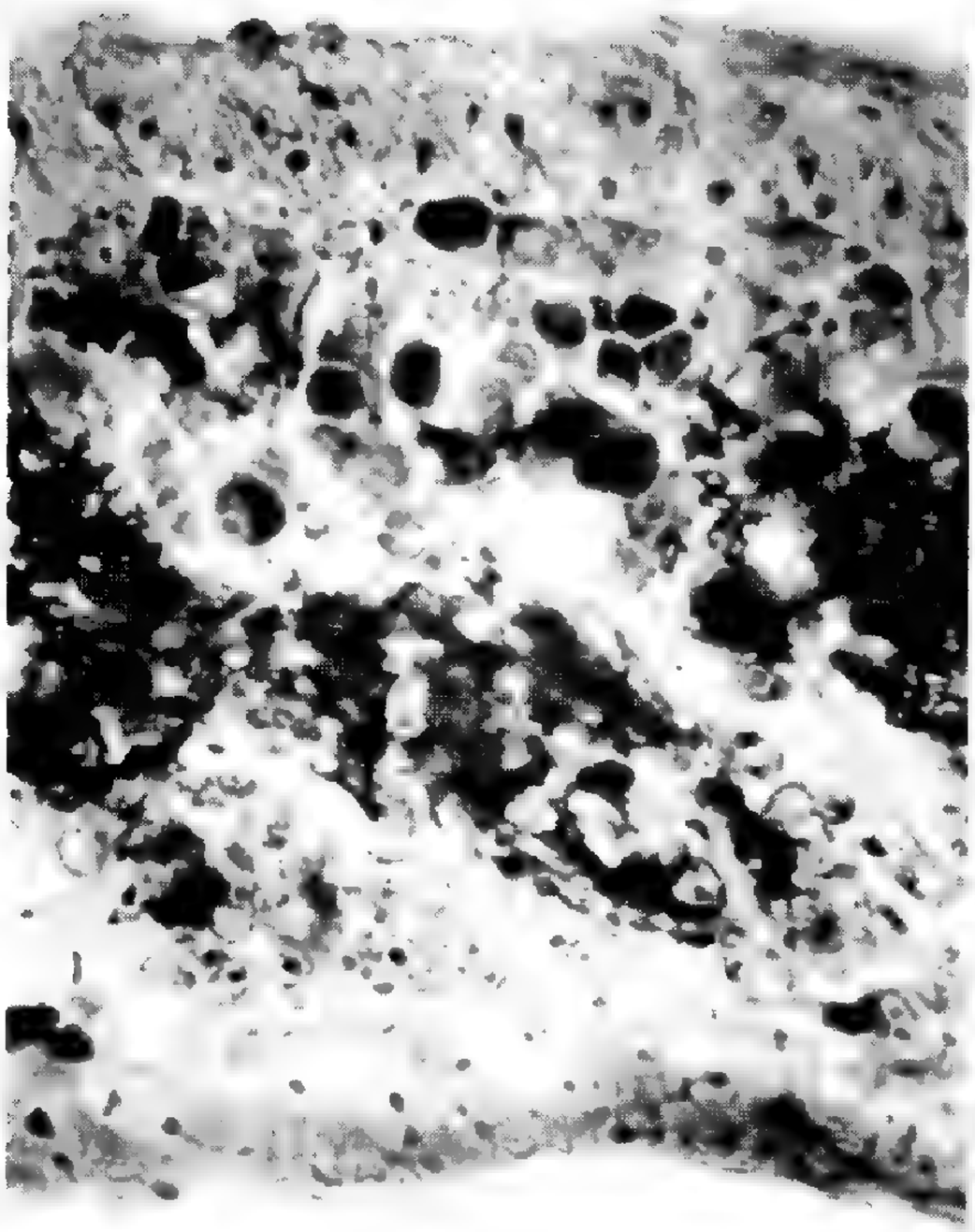

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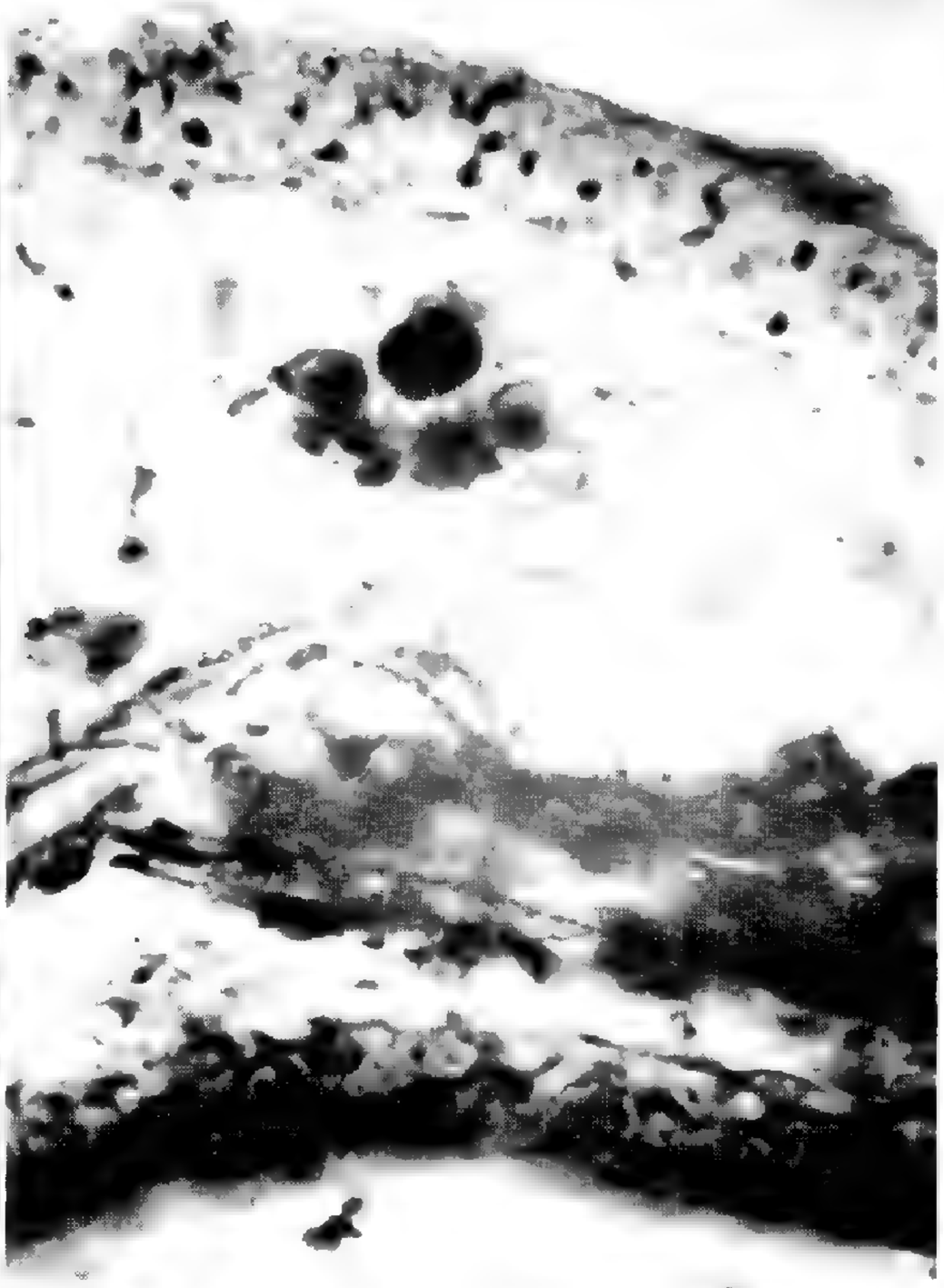
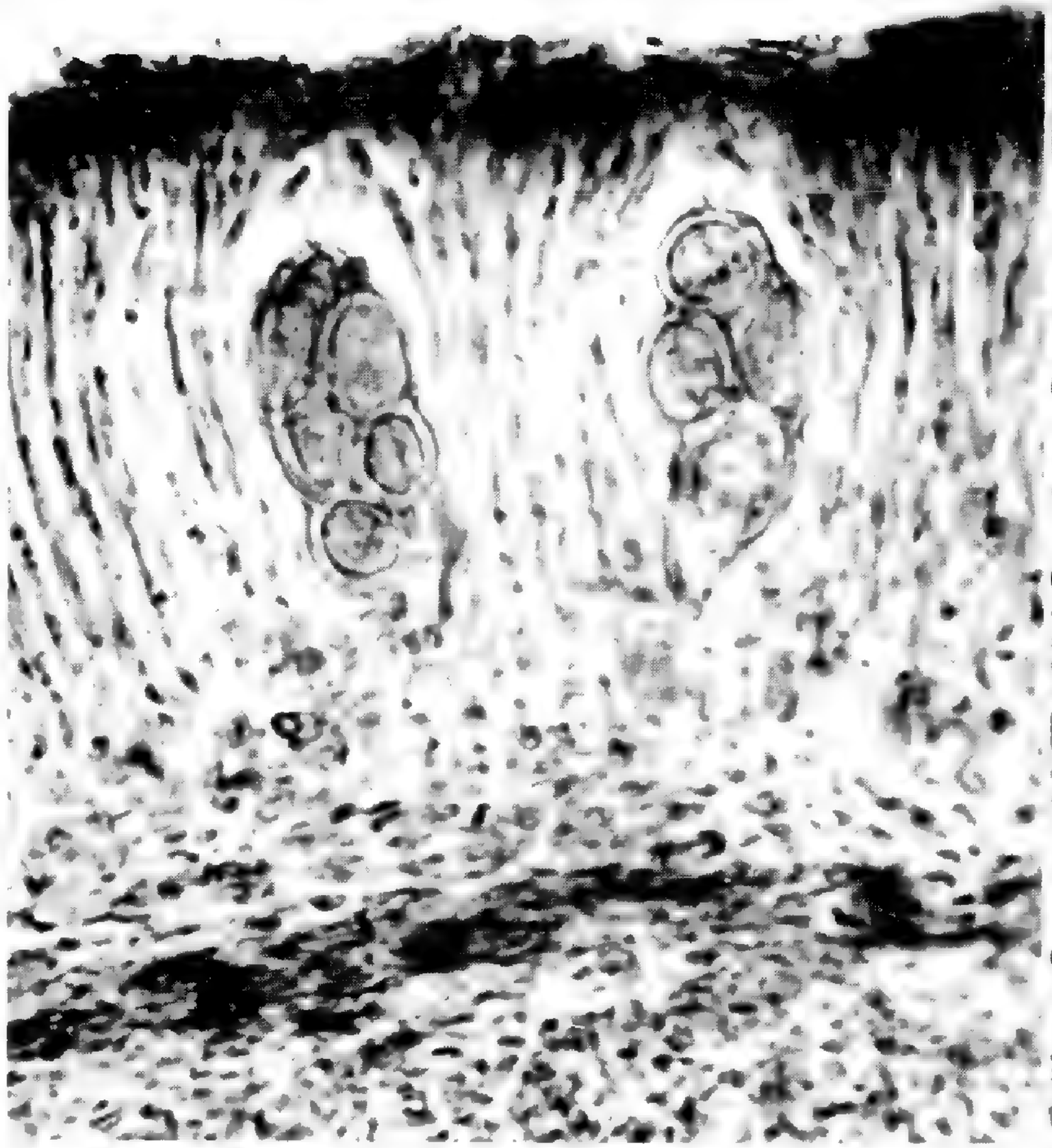


Anatomical structure of the upper cortex in *Cetrelia* and *Platismatia:* 41. Prosoplectenchymatous cortex of *C. chicitae* (Culb.) Culb. & Culb. 42. Same, *C. nuda* (Hue) Culb. & Culb. 43. Prosoplectenchymatous upper cortex of *P. glauca* (L.) Culb. & Culb. 44. Same, *P. tuckermanii* (Oakes) Culb. & Culb. All photographs ×300.

45



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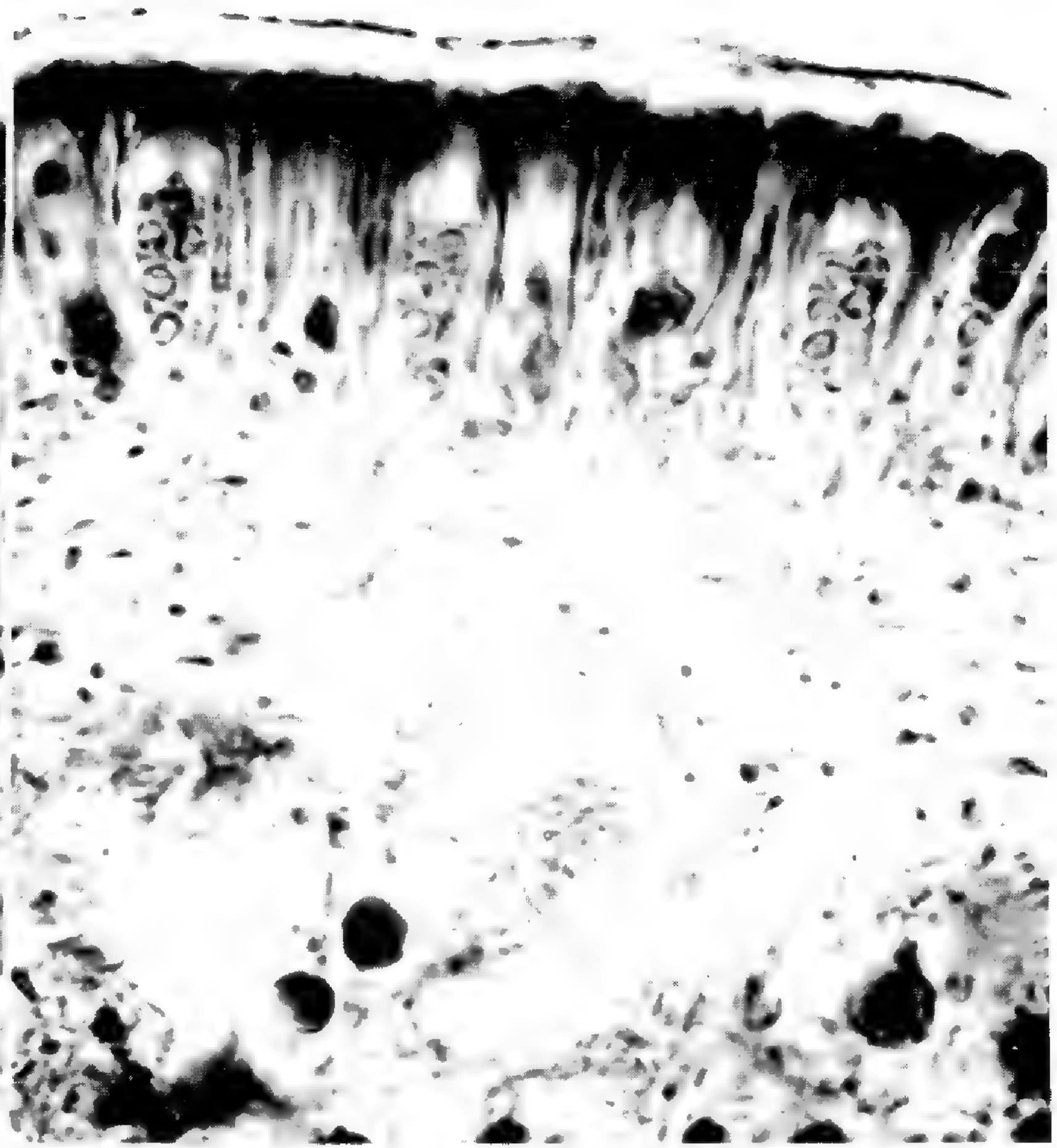
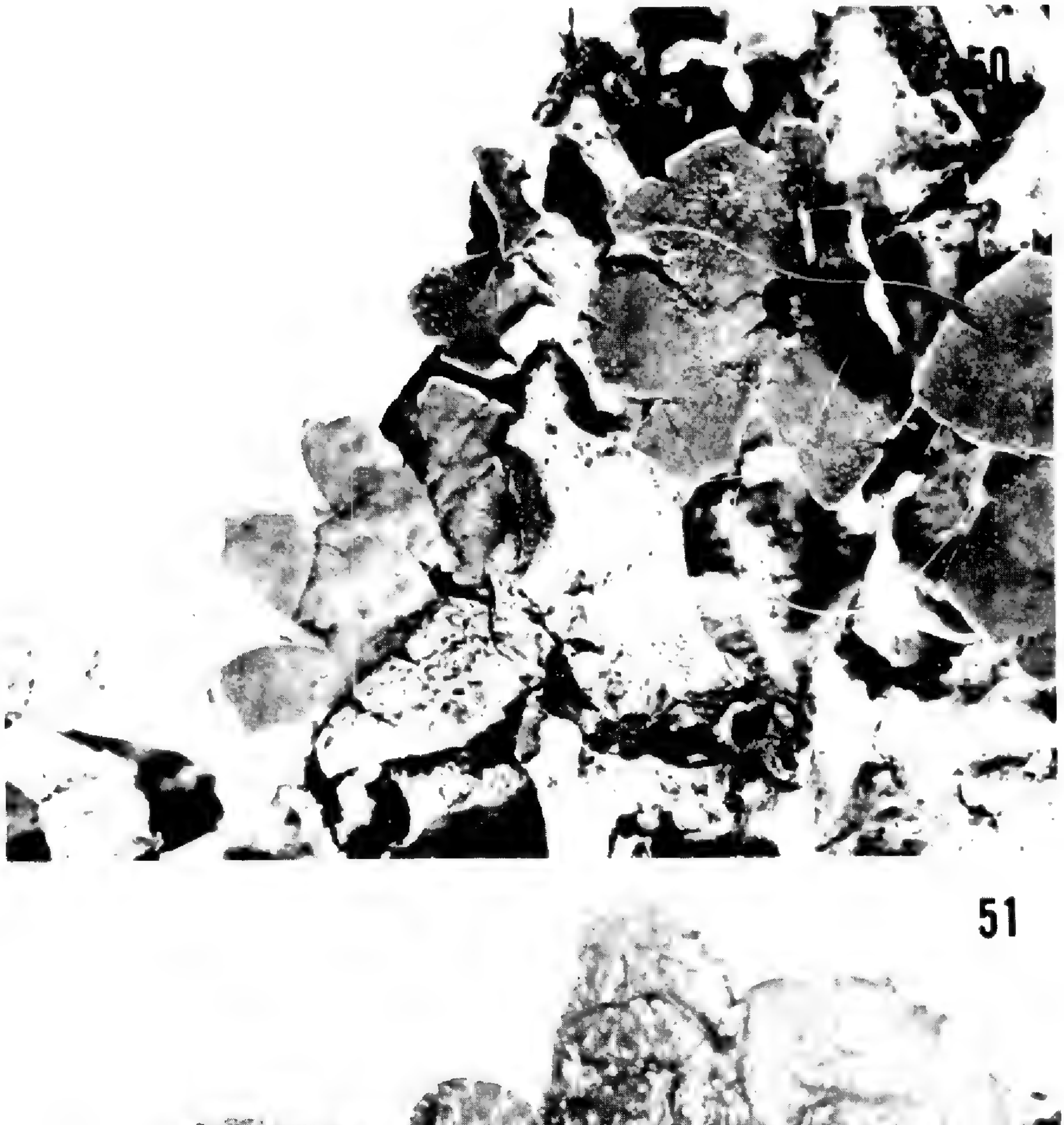


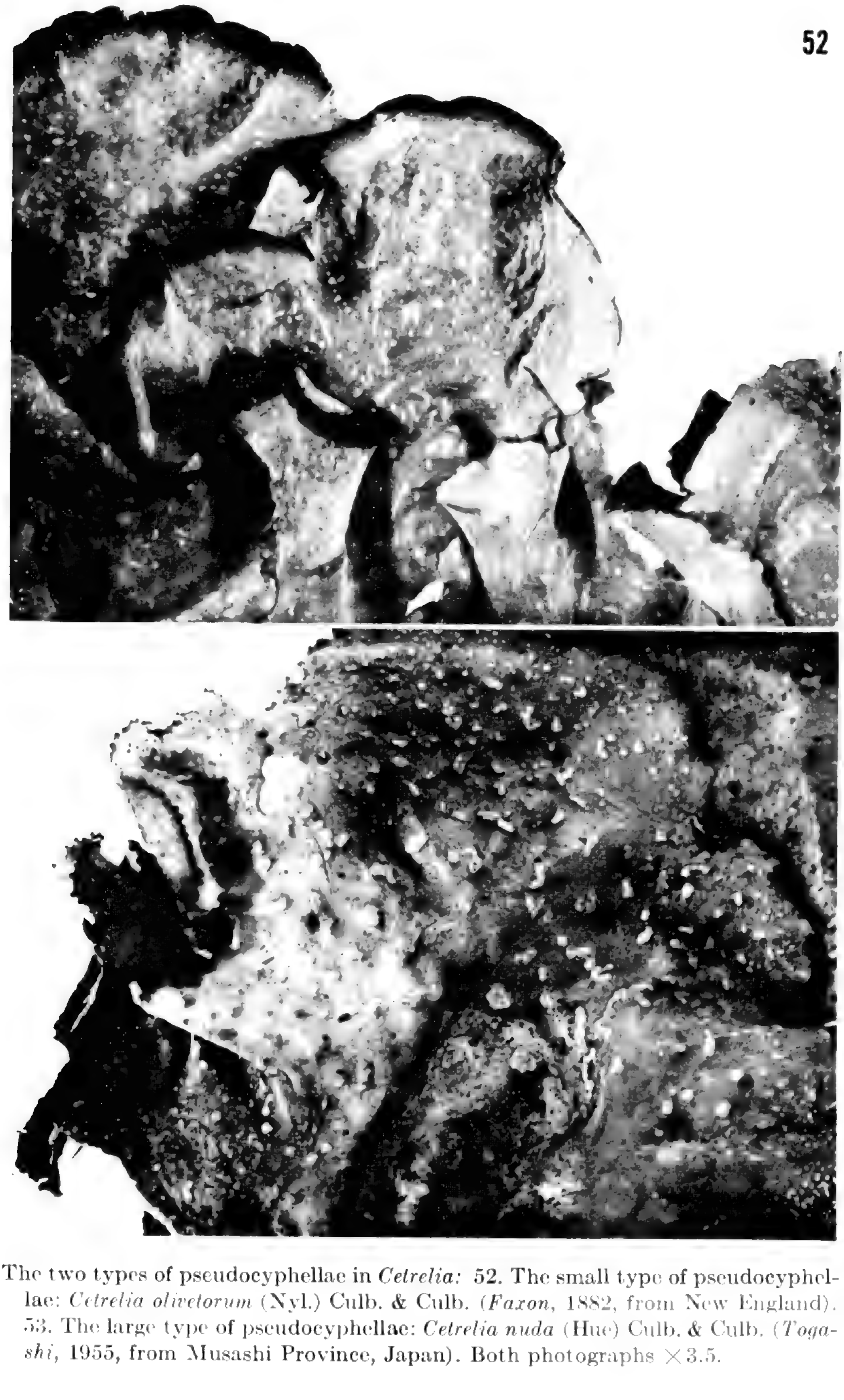
The hymenium, asci, and ascospores of *Cetrelia* and *Platismatia:* 45. *C. nuda* (Hue) Culb. & Culb. showing the large asci with large ascospores typical of the genus. ×480. 46. *P. glauca* (Oakes) Culb. & Culb. showing the small asci with small ascospores typical of the genus. ×480.

Laminal and submarginal apothecia in *Cetrelia:* 47. Immature apothecia of *C. cetrarioides* (Del. ex Duby) Culb. & Culb. (*Culberson & Culberson* 11563, from Merionethshire, Wales) ×8. 48. Apothecia of *C. nuda* (Hue) Culb. & Culb. (*Asahina*, 1934, from Mt. Fuji, Japan) ×4. 49. Apothecium and marginal pycnidia of *C. nuda* (Hue) Culb. & Culb. (*Togashi*, 1955, from Yamoto Province, Japan) ×6.

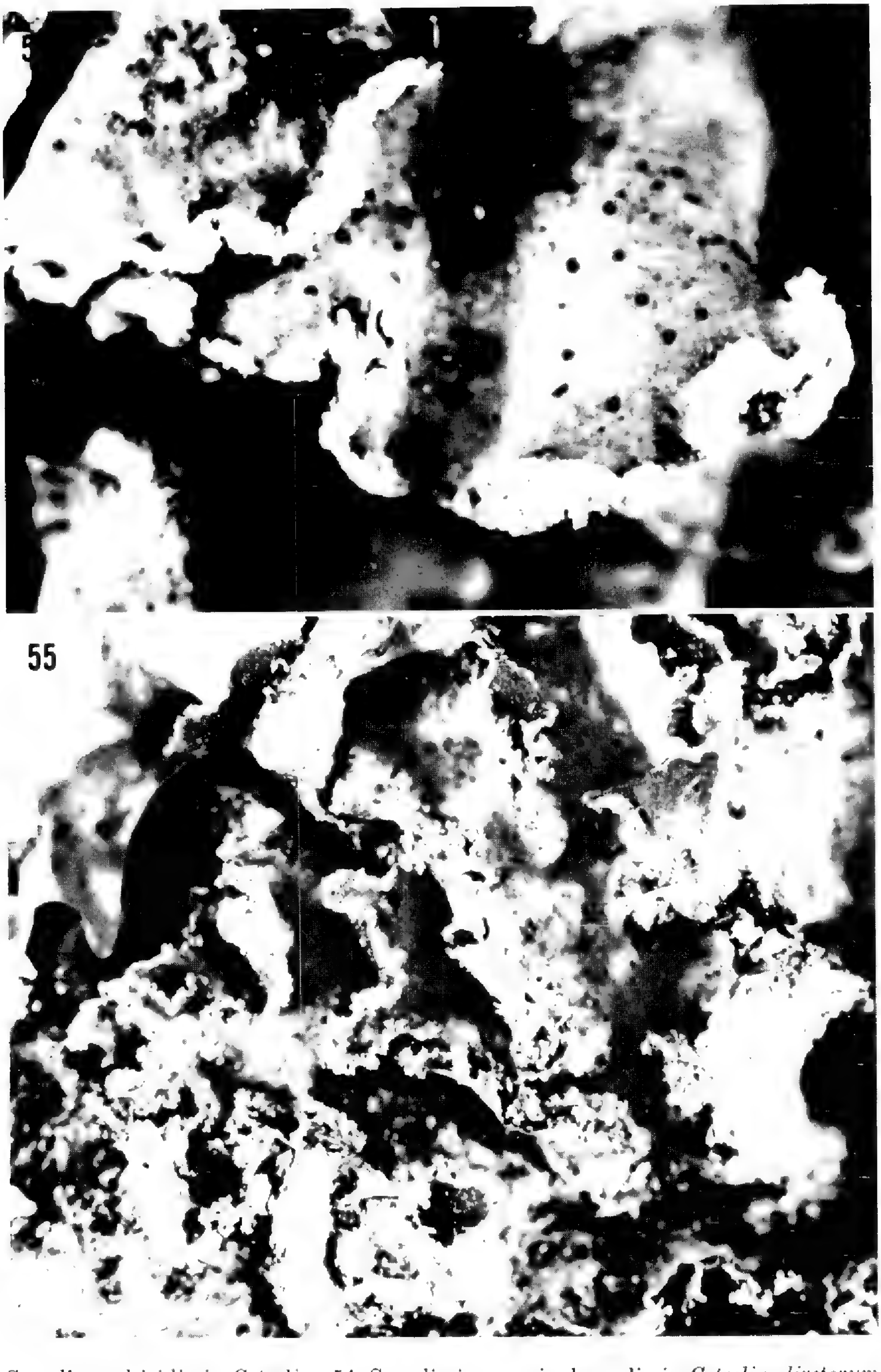


50. Perforate apothecia of *Cetrelia davidiana* Culb. & Culb. (*Handel-Mazzetti* 4254, from Yunnan Province, China) ×3.7. 51. Punctate lower cortex of *Platismatia erosa* Culb. & Culb. (*Awasthi* 2292, from Nepal) ×6.

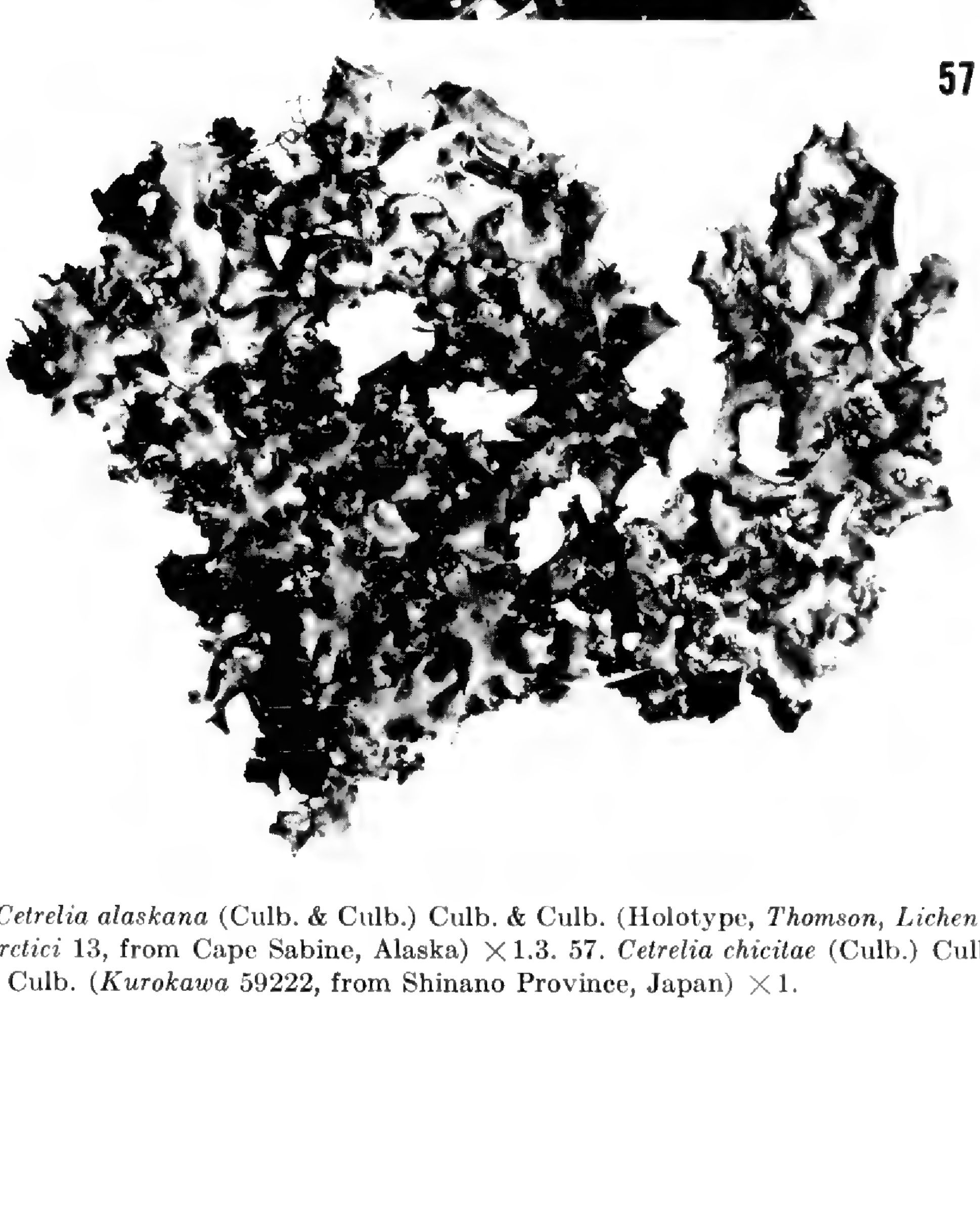
52



The two types of pseudocyphellae in *Cetrelia:* 52. The small type of pseudocyphellae: *Cetrelia olivetorum* (Nyl.) Culb. & Culb. (*Faxon*, 1882, from New England). 53. The large type of pseudocyphellae: *Cetrelia nuda* (Hue) Culb. & Culb. (*Togashi*, 1955, from Musashi Province, Japan). Both photographs ×3.5.



Soredia and isidia in *Cetrelia:* 54. Soredia in marginal soralia in *Cetrelia olivetorum* (Nyl.) Culb. & Culb. (*Lichenotheca Polonica* 174, from Poland) ×7. 55. Isidia in *Cetrelia braunsiana* (Müll. Arg.) Culb. & Culb. (*Togashi*, 1956, from Echigo Province, Japan) ×7.



56. *Cetrelia alaskana* (Culb. & Culb.) Culb. & Culb. (Holotype, *Thomson, Lichenes Arctici* 13, from Cape Sabine, Alaska) ×1.3. 57. *Cetrelia chicitae* (Culb.) Culb. & Culb. (*Kurokawa* 59222, from Shinano Province, Japan) ×1.

58

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58. *Cetrelia braunsiana* (Müll. Arg.) Culb. & Culb. (*Togashi*, 1956, from Echigo Province, Japan) ×2. 59. *Cetrelia cetrarioides* (Del. ex Duby) Culb. & Culb. (*Culberson & Culberson* 11564, from Merionethshire, Wales) ×0.8.

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60. *Cetrelia davidiana* Culb. & Culb. (*Handel-Mazzetti* 4254, from Yunnan Province, China) ×1.3. 61. *Cetrelia delavayana* Culb. & Culb. (Isotype, *Delavay*, 1888, from Yunnan Province, China) × 1.5.

62

62. *Cetrelia isidiata* (Asah.) Culb. & Culb. (*Kurokawa* 331, from Formosa) ×1.
63. *Cetrelia japonica* (Zahlbr.) Culb. & Culb. (*Kurokawa* 58374, from Shinano Province, Japan), showing detail of the lobulae ×5.

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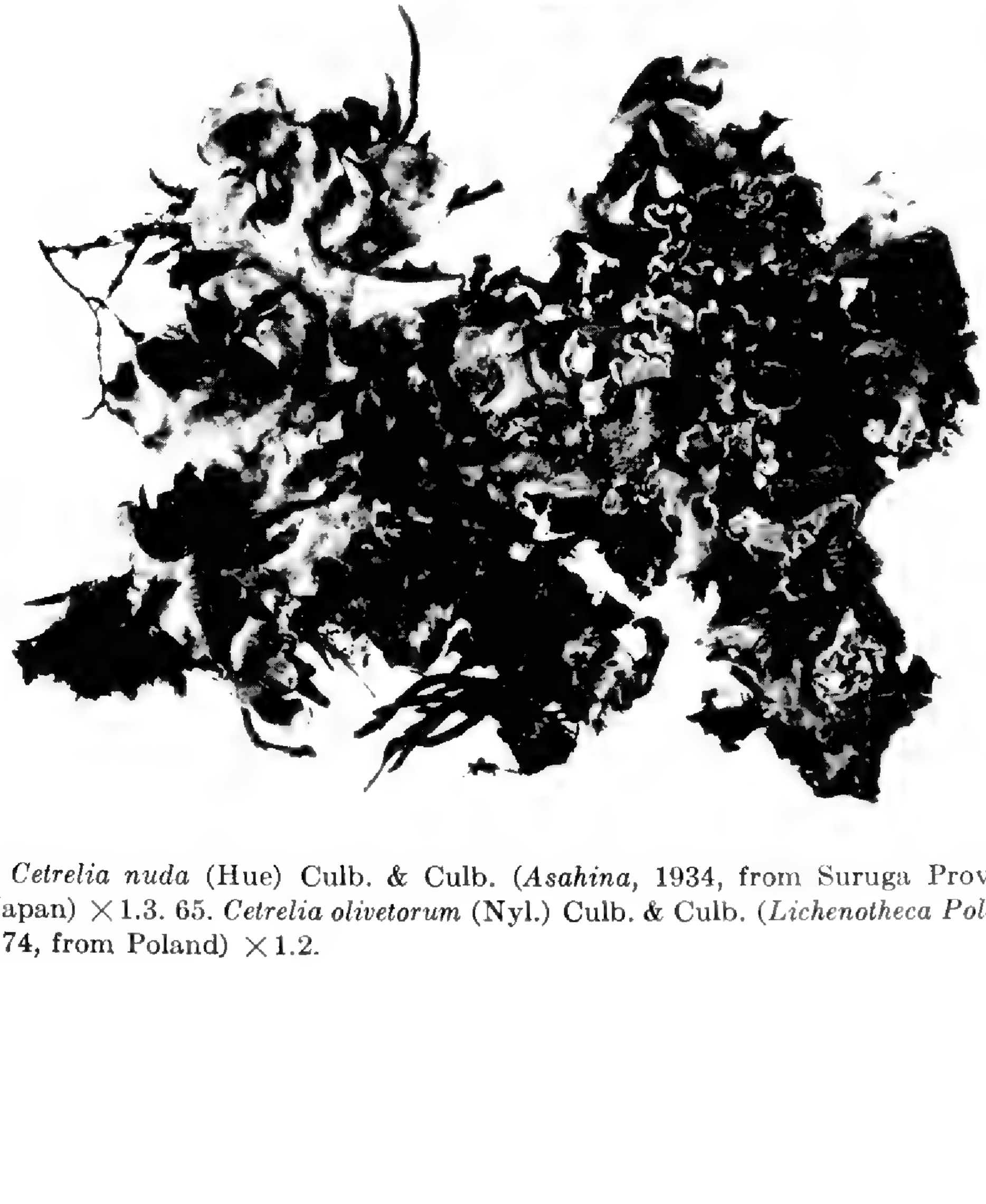

64. *Cetrelia nuda* (Hue) Culb. & Culb. (*Asahina*, 1934, from Suruga Province, Japan) ×1.3. 65. *Cetrelia olivetorum* (Nyl.) Culb. & Culb. (*Lichenotheca Polonica* 174, from Poland) ×1.2.

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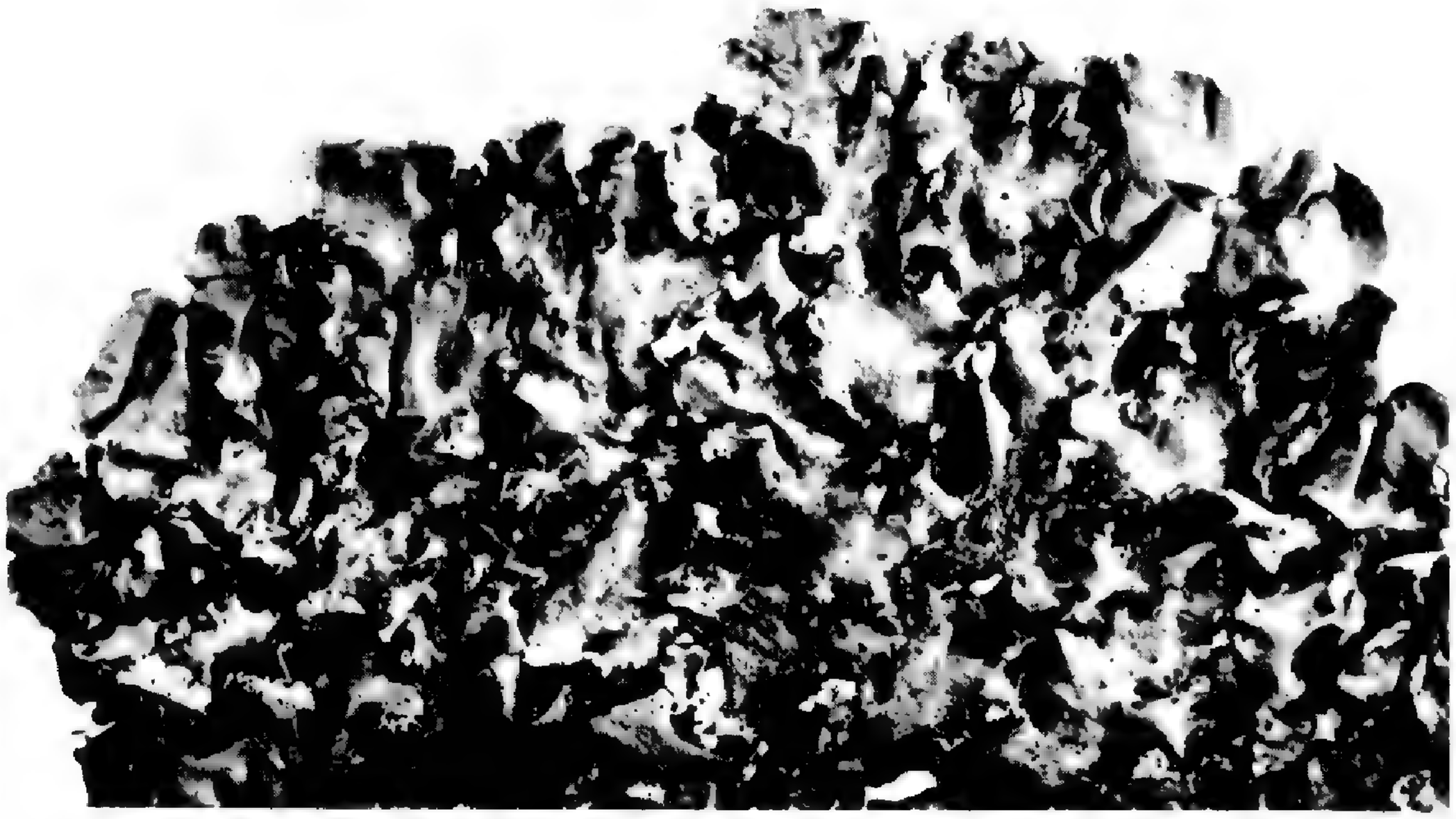

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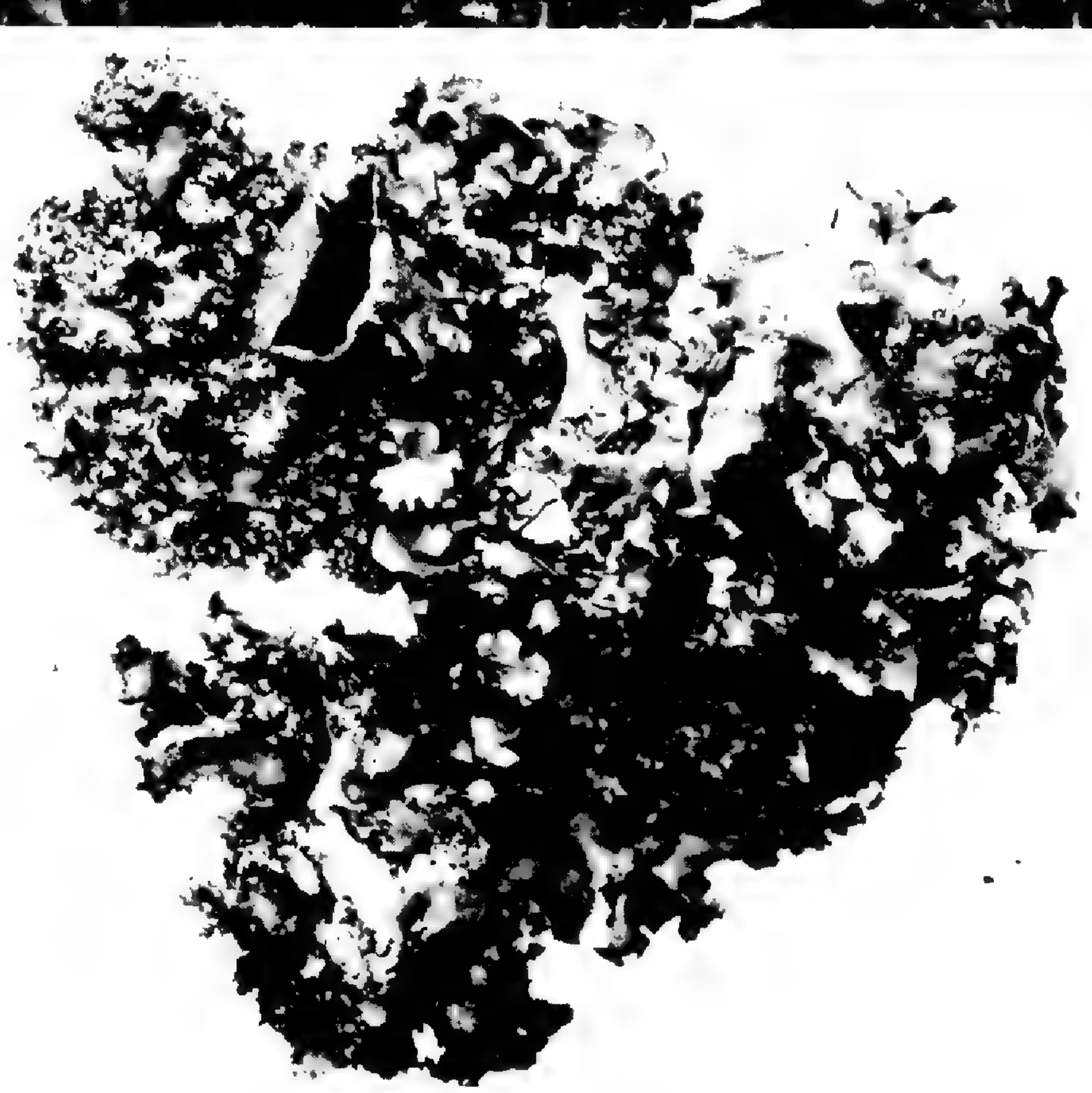
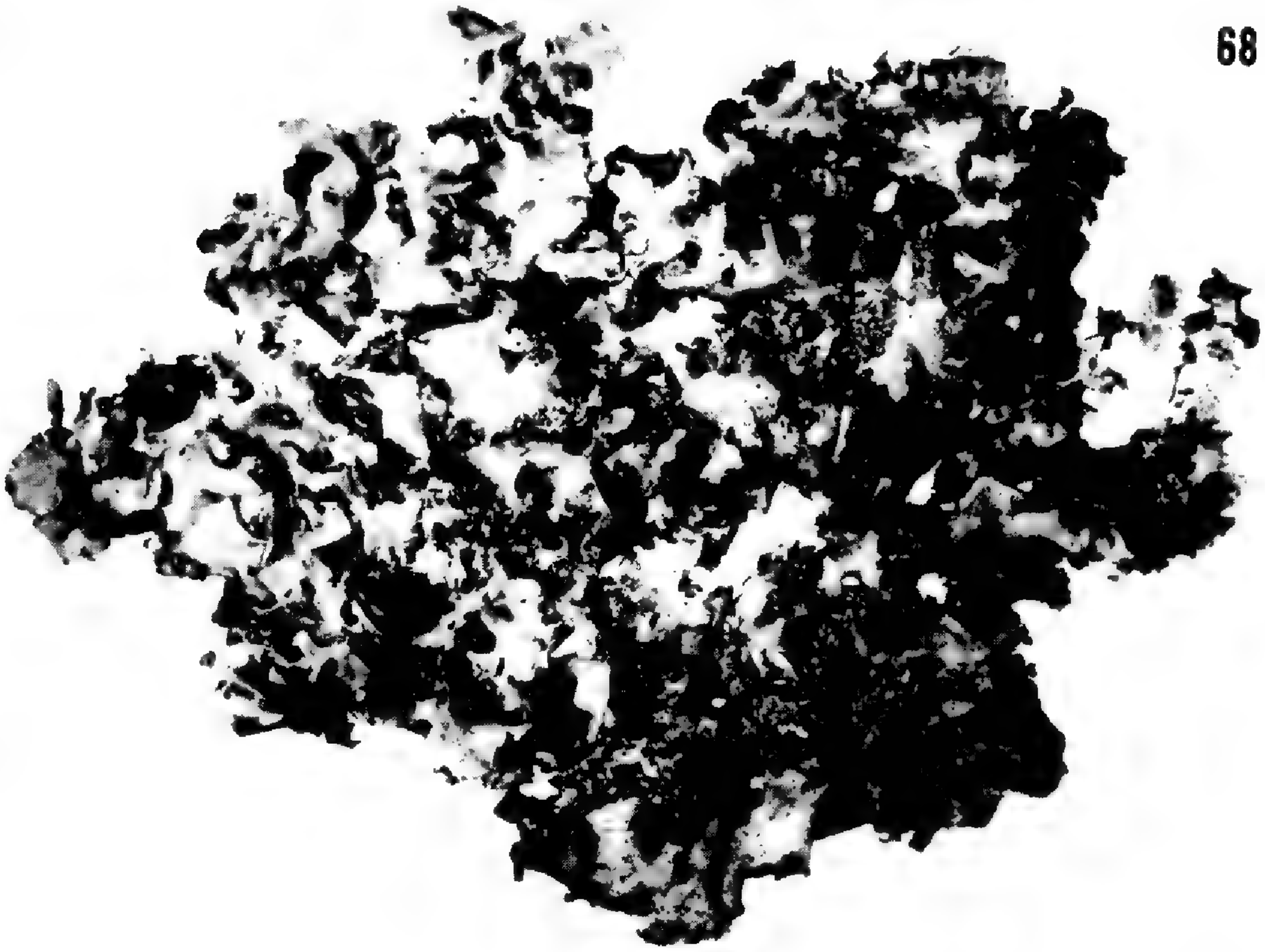


66. *Cetrelia pseudolivetorum* (Asah.) Culb. & Culb. (*Kurokawa* 137, from Formosa) ×1. 67. *Cetrelia sanguinea* (Schaer.) Culb. & Culb. (*Du Rietz*, 1927, from Java) ×1.2.

68



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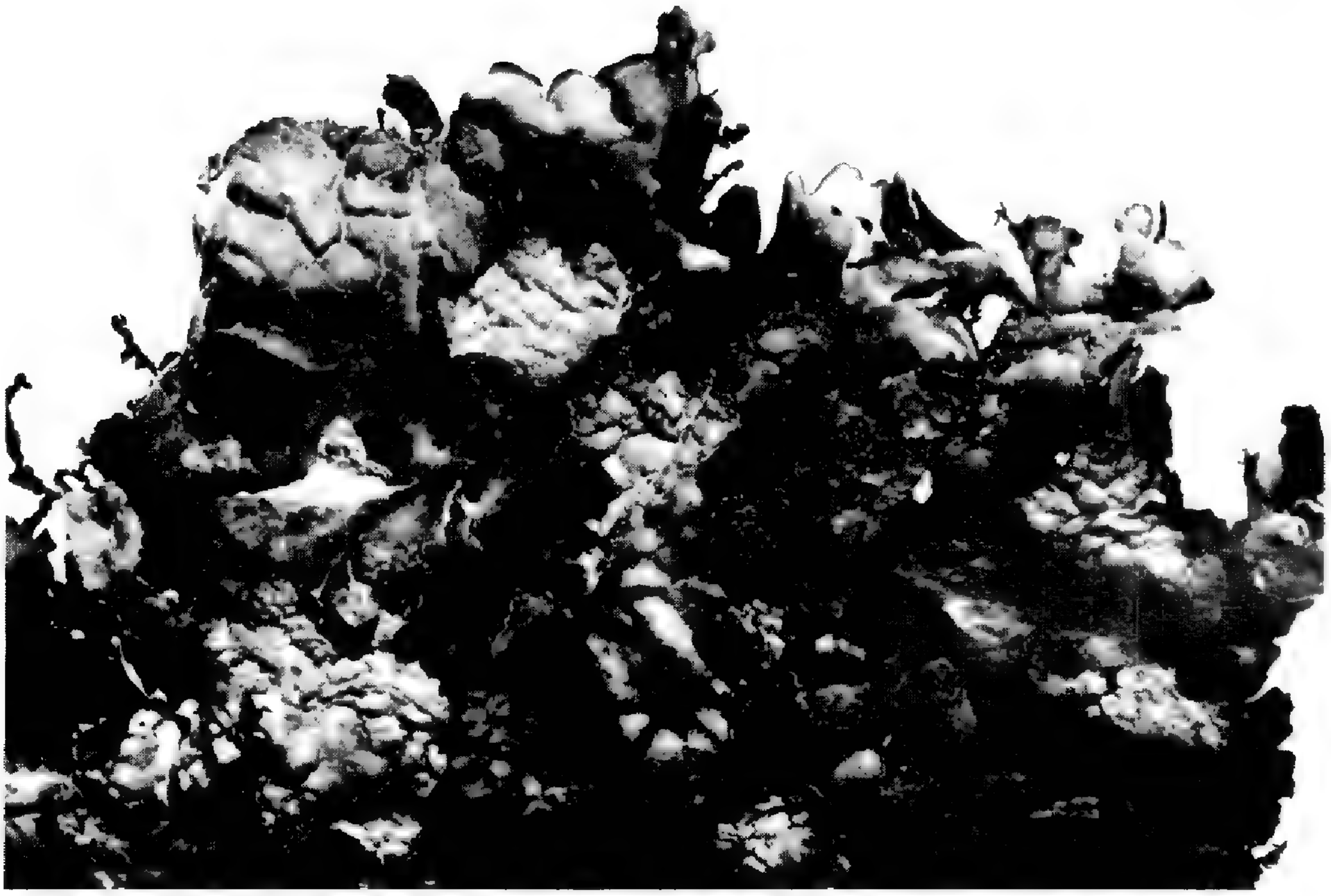

68. *Cetrelia sinensis* Culb. & Culb. (*Kurokawa* 449, from Formosa) ×1.5. 69. *Platismatia erosa* Culb. & Culb. (*Poelt* L37, from Nepal) ×2.

70

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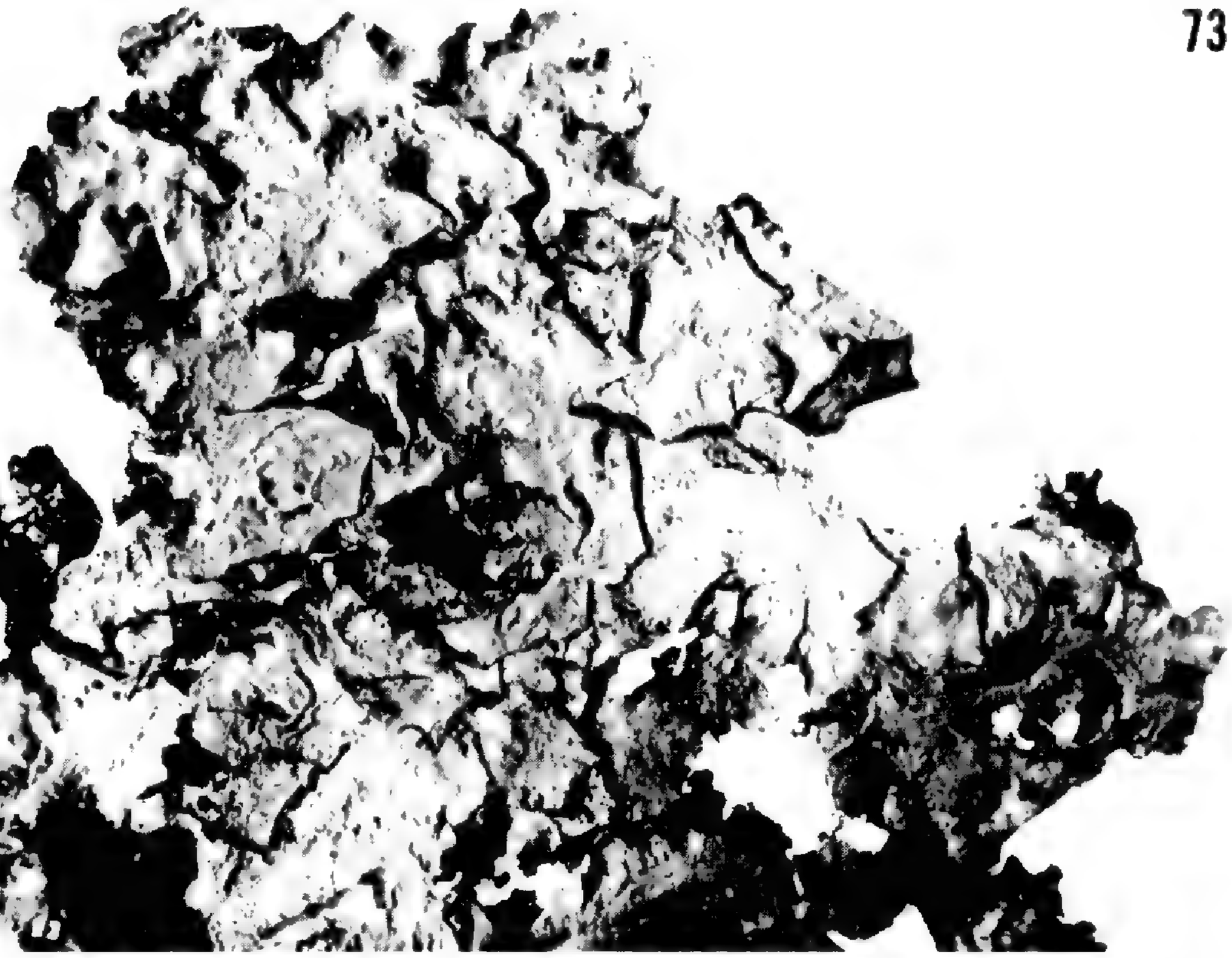
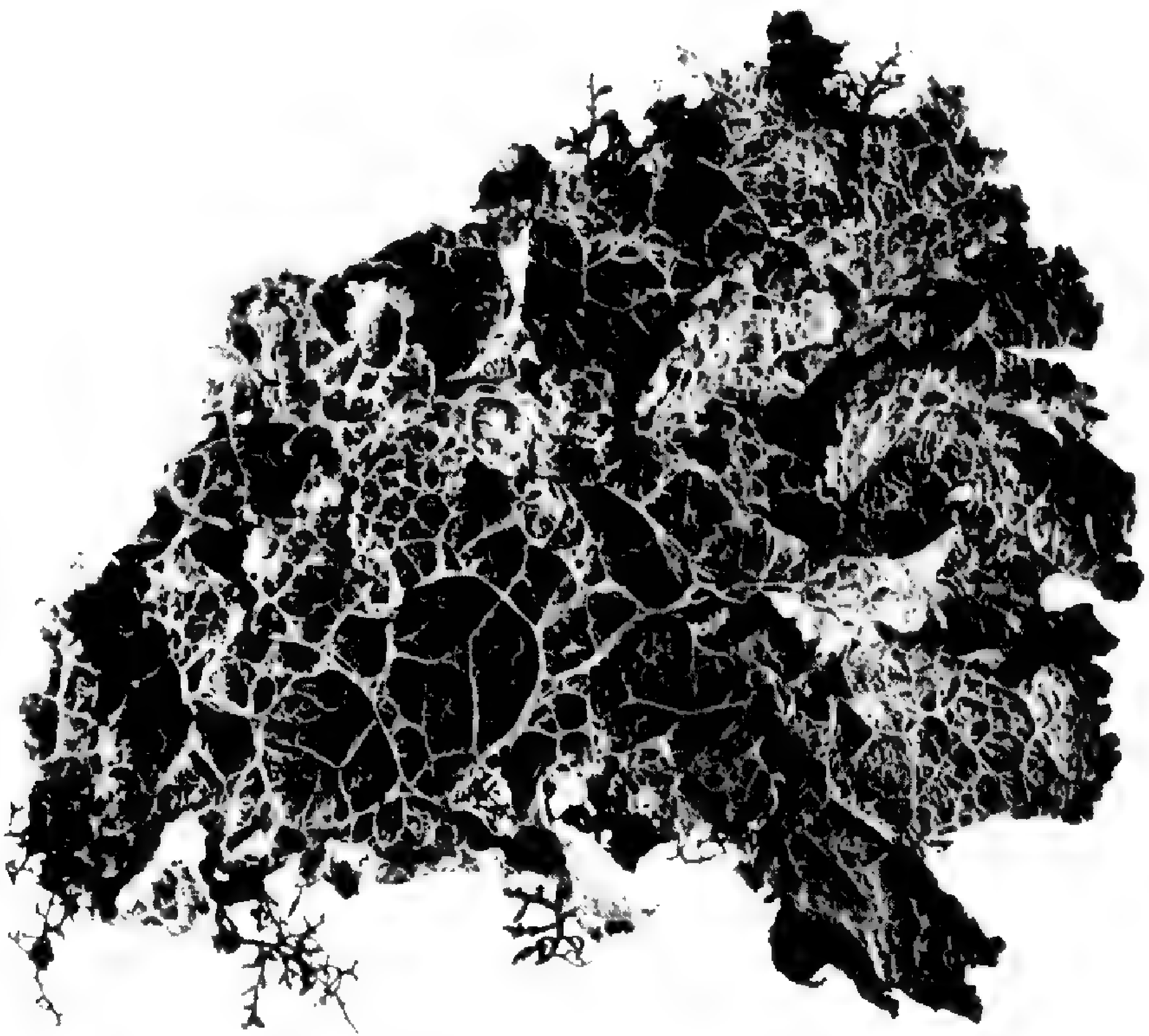
Platismatia glauca (L.) Culb. & Culb. (two forms): 70. With fruticose branchlets (*Stickney* 1005b, from Montana) ×2.5. 71. With sorediate lobes (*Imshaug* 26501, from Quebec Province, Canada) ×1.1.



72. *Platismatia herrei* (Imsh.) Culb. & Culb. (Lectotype, *Hall*, 1871, from Oregon) ×1. 73. *Platismatia interrupta* Culb. & Culb. (*Culberson & Culberson* 10669, from Suruga Province, Japan) ×1.5.

74



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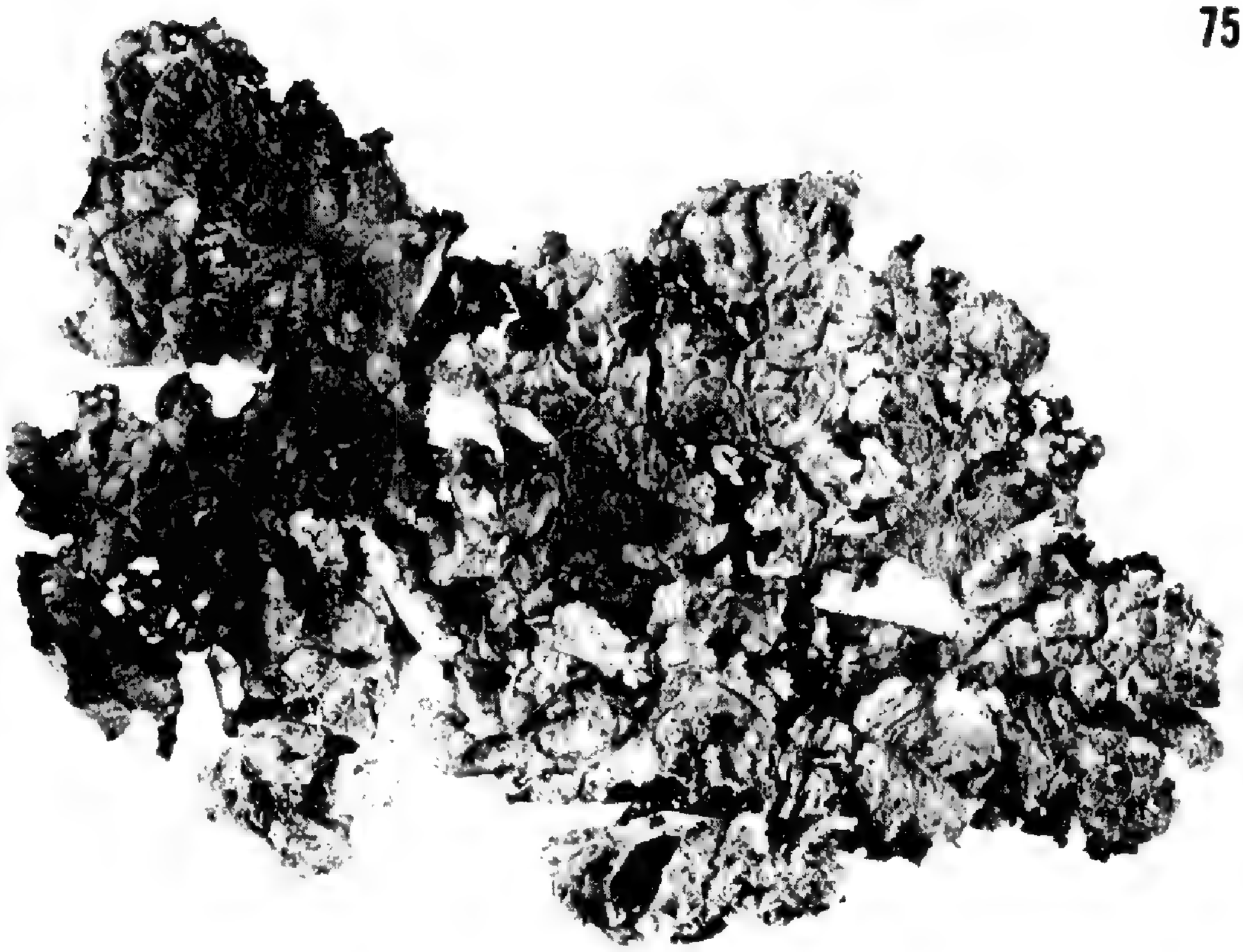
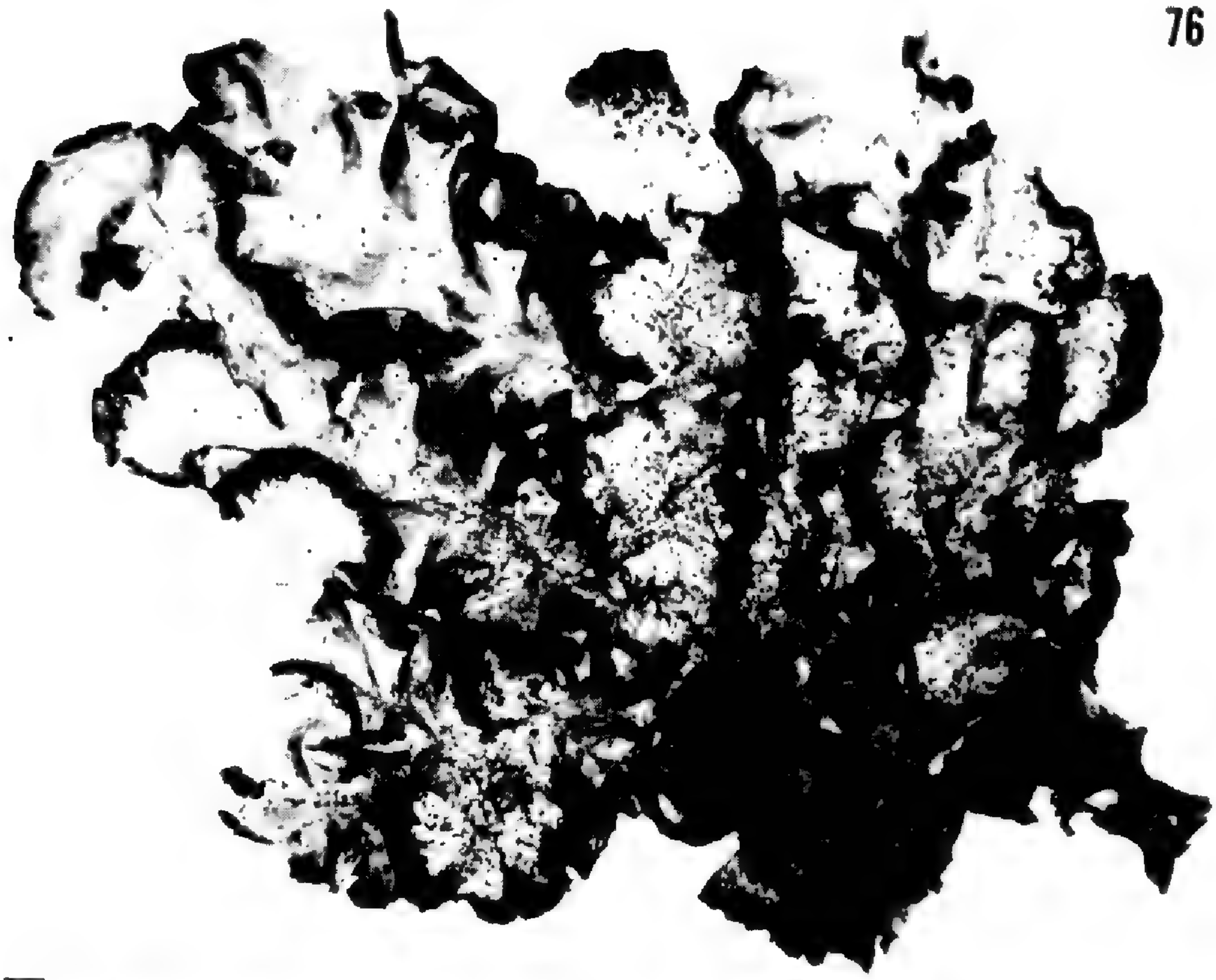


74. *Platismatia lacunosa* (Ach.) Culb. & Culb. (*Eyerdam*, 1947, from Alaska) ×1.3.
75. *Platismatia norvegica* (Lynge) Culb. & Culb. (*Szczawinski* V.I./558, from Vancouver Island, British Columbia, Canada) ×1.



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76. *Platismatia regenerans* Culb. & Culb. (Holotype, *Hale* 28207, from Sabah) ×2. 77. *Platismatia stenophylla* (Tuck.) Culb. & Culb. (Holotype, *Bolander* 384, from California) ×0.9.

78

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78. *Platismatia tuckermanii* (Oakes) Culb. & Culb. (*Moore* 1372, from North Carolina) ×1.3. 79. *Platismatia formosana* (Zahlbr.) Culb. & Culb. (*Suzuki*, 1935, from Formosa) ×2.

7. Cetrelia delavayana Culb. & Culb., sp. nov. PLATE 16

Thallus mediocris, 7–10 cm. latus; laciniae 1.3–1.7 cm. latae. Superficies superior sordide citrella apud exemplaria vetera herbarii (albida apud plantas vivas?), levis, pseudocyphellata, pseudocyphellis punctatis, paucis, parvissimis. Superficies inferior picea, marginibus castanea, nonnihil punctata, leviter rhizinata. Cortex superior 16–22μ crassus; medulla 101–186μ crassa; cortex inferior (12–)16–23μ crassus. Apothecia ad 0.8 cm. lata, perforata, excipulo thallino dense pseudocyphellato; hymenium 62–109μ crassum; strata subhymenialia 43–78μ crassa, supra hyalina et subtus aurea. Sporae 8-nae, ellipsoideae, 16–24$\times$ 9–12μ. Pycnidia magna, marginalia, non stipitata; conidia ca. 1.5$\times$ 6.0μ, recta, extremis nonnihil inflatis.

Thallus medium, 7–10 cm. broad; lobes 1.3–1.7 cm. broad. Upper surface pale brownish in old herbarium specimens (whitish when fresh?), smooth, pseudocyphellate, the pores few, very small, rarely reaching 0.5 mm. Lower surface jet-black, the margins dark brown, somewhat punctate in some specimens; rhizines few. Upper cortex 16–22μ thick, medulla 101–186μ thick; lower cortex (12–)16–23μ thick. Apothecia to 0.8 cm. broad, perforate, the thalloid exciple densely pseudocyphellate; hymenium 62–109μ thick; subhymenial layers 43–78μ thick, hyaline above and golden yellow below. Spores 8, ellipsoid, 16–24$\times$9–12μ. Pycnidia large, marginal, unstalked; conidia about 1.5$\times$6.0μ, rod-shaped, the ends often somewhat inflated.

TYPE.—"Au col de Lopin-chan," Yunnan, China, *Delavay*, 1888 (PC, holotype).

MEDULLARY REACTIONS.—K—, C—, KC— or KC+ pinkish, P—.

CONSTITUENTS.—Imbricaric acid and atranorin.

DISTRIBUTION (Map, Figure 21).—In the mountains of Szechwan and Yunnan, China; on the bark of trees and shrubs.

Cetrelia delavayana can be distinguished from most other esorediate and nonisidiate species of the genus both morphologically, by the presence of small pseudocyphellae rather than large aggregate ones, and chemically by the presence of perlatolic acid. *Cetrelia collata* produces imbricaric acid and inhabits much the same range but has very large pores exceeding 1 mm. *Cetrelia alaskana* has small pores and imbricaric acid, its habit is completely different, and its range is the western coast of Alaska.

CHEMICAL ANALYSIS.—Eight samples of this species were tested. All showed perlatolic acid and atranorin. Four residues were hydrolyzed and showed no trace of divaric acid, indicating the absence of imbricaric acid, but at least two samples gave a KC+ reaction which could not be associated with identifiable crystals or chromatographic spots. It is possible that this unidentified KC+ accessory compound is the

same as that which gives a KC+ reaction in other *Cetrelia* species which contain acid.

SPECIMENS EXAMINED:

CHINA: SZECHWAN: Mt. Lose-chan, south of Ningyüen, 3,950 m., *Handel-Mazzetti* 1441 (WU).

YUNNAN: Yangtze watershed, Likiang, Likiang Snow Range, *Rock* 11775 (W); Lenago Pass between Mekong and Yangtse, 27°43′N, *Gebauer*, 1914 (TNS, W, WU); between Dali (Talifu) and Hodjing, above Hsiang-schuiho, 26°15′N, 3,400 m., *Handel-Mazzetti* 7398 (W); Lopin-chan Pass, *Delavay*, 1888 (PC, 2 collections).

8. Cetrelia isidiata (Asah.) C. & Culb., comb. nov. PLATE 17

Cetraria sanguinea Schaer. f. *isidiata* Asah. *in* Sato, Parmeliales (I), in Nakai & Honda, Nova Fl. Jap. 73. 1939. Type: Japan, Honshu, Titibu [=Chichibu], Mt. Kobushi, *Asahina*, 1933 (TNS, holotype).

Thallus small to large, 5–19 cm. broad; lobes 0.5–1.5 cm.broad. Upper surface grayish or uniformly light brown in old herbarium specimens, pseudocyphellate, the pores tiny and infrequent, isidiate, the isidia mostly marginal, globose to somewhat coralloid or slightly branched, or poorly developed and very infrequent altogether. Lower surface jet-black, the margins brown, punctate or not; rhizines conspicuous but unevenly distributed. Upper cortex 16–31μ thick; medulla 84–217μ thick; lower cortex 13–31μ thick. Apothecia and pycnidia unknown.

MEDULLARY REACTIONS.—K−, C+ red, PD−

CONSTITUENTS.—Anziaic acid and atranorin.

DISTRIBUTION (Map, Figure 8).—Honshu, Japan, and Formosa; on trees.

The only other C+ isidiate species that *Cetrelia isidiata* might be mistaken for is *C. pseudolivetorum* which contains olivetoric acid and reacts to produce a pink color with this reagent. A chemical test is desirable for the identification of these species since the thallus spot tests may be somewhat variable.

The original classification of the present taxon as a variety of the Javanese species *sanguinea* is not tenable even though both produce anziaic acid in the medulla. The Javanese plants lack isidia, have very large pseudocyphellae that become confluent, and usually bear apothecia, while the Japanese and Formosan ones have isidia and minute pseudocyphellae and are unknown in fruit. *Cetrelia isidiata* seems to be a very well defined species, more closely related to *C. chicitae*, for example, than to *C. sanguinea*.

The single Formosan collection examined (Plate 17) is rich and well developed, but it shows a very meager production of isidia as do the Japanese specimens. Since only a few collections of this species are known, it is impossible to give a definitive assessment of the importance of isidia as a diagnostic trait; in fact they may be of little conse-

quence. It is, therefore, with some hesitation that we take up *isidiata* as the specific epithet, a name given by Asahina to the taxon when he considered it a forma of the species treated in this monograph as *Cetrelia sanguinea*. Isidia are much less well developed in the present species than in *C. braunsiana*, for example.

CHEMICAL ANALYSIS.—The four known specimens of this species were tested, and all contained atranorin (proved in the GA*o*-T solution) and anziaic acid (identified by paper chromatography).

ADDITIONAL SPECIMENS EXAMINED:

JAPAN: HONSHU: Chichibu, Mt. Kobushi, *Asahina*, 1933 (TNS, original collection; 3 specimens).

FORMOSA: Mt. Shin-Kao-San, Mt. Shi-San, 3,300–3,600 m., *Kurokawa* 311 (TNS).

9. Cetrelia japonica (Zahlbr.) Culb. & Culb., comb. nov. PLATE 17

Cetraria japonica Zahlbr., Annal. Mycol. 14:60. 1916. Type: Japan, Prov. Kotsuke, Mt. Akagi, *Yasuda* (W, lectotype).

Platysma collatum f. *microphyllinum* Hue, Nouv. Arch. Mus., IV, 1:209. 1899. Type: Japan, Fujiyama, *Faurie* 519 (PC, lectotype).

Cetraria collata f. *microphyllina* (Hue) Zahlbr. Catal. Lich. Univ. 6:285. 1930.

Thallus medium to very large, 10–28 cm. broad; lobes 0.5–1.5 cm. broad, the margins densely fringed with multibranched lobulae, narrow and isidioid or more broadly expanded and lobelike, in some specimens becoming so abundantly developed as to make the lichen appear cristate. Upper surface grayish-white or ashy-white (or light brownish in old herbarium specimens), smooth, pseudocyphellae conspicuous, punctiform to elongate but rarely reaching 1 mm. in size. Lower surface jet-black, a marginal zone near the tips of the lobes chestnut brown or even whitish, not punctate; rhizines black. Upper cortex 18–23μ thick, interspersed with abundant crystals; medulla 83–171μ thick; lower cortex 16–23μ thick, without crystals, darkening. Apothecia very rare, submarginal, often perforate, 0.4–1.3 cm. broad; hymenium 65–70μ thick; subhymenial layers 47–57μ thick, underlain by a thick continuous zone of algae. Spores 8, ellipsoid, 14–21$\times$8–11μ. Pycnidia very rare, large, black, emergent, about 0.1 mm. broad, restricted to the marginal lobulae, the ostiole prominent; conidia 1.5$\times$5μ, rod-shaped, the ends somewhat enlarged.

MEDULLARY REACTIONS.—K−, C−, KC− or KC+ pink, PD−.

CONSTITUENTS.—Microphyllinic acid and atranorin.

DISTRIBUTION (Map, Figure 16).—The mountains of Hokkaido and Honshu in Japan, South Korea, Formosa, northern Sabah (Borneo), and Java.

Cetrelia japonica is chemically distinct from all the other species of the genus in the production of microphyllinic acid. Morphologically, however, it could be mistaken for *C. sinensis* (with imbricaric acid), *C.*

sanguinea (with anziaic acid), or *C. pseudolivetorum* (with olivetoric acid). While its distinction from *C. sinensis* is probably purely chemical, the morphology of the whole population of *C. japonica* is apparently somewhat different from that of the populations of *C. sanguinea* and *C. pseudolivetorum*, although it must be admitted that many individual specimens of all these species cannot be identified without chemical tests. As a rule the margins of the lobes of *C. japonica* are moderately to densely fringed with tiny lobulae or dorsiventral isidia. *Cetrelia pseudolivetorum* and *C. sanguinea* also have similar lobulae, but as a rule the lobulae are less well developed, and many thalli, especially in *C. sanguinea*, may lack them altogether.

The population assigned herein to *Cetrelia japonica* may represent two taxa. The only known Javanese specimen has only true isidia rather than lobulae. It may be a rare Javanese endemic, but it is assigned to *C. japonica* provisionally because such isidia can be found (with lobulae) on some specimens of *C. japonica* from Japan, because the Javanese plant produces microphyllinic acid (a rare chemical trait in the genus), and because typical specimens of *C. japonica* are known from nearby Sabah.

CHEMICAL ANALYSIS.—This species contains the rare lichen substance microphyllinic acid. Twenty-two samples were tested, and all but two showed atranorin in either the GE or the GA*o*-T solutions. But microphyllinic acid seems to interfere with the crystal tests for atranorin so that often it is necessary to allow the slides to stand overnight before crystals of atranorin are observable in the GA*o*-T solution. The two samples which seem to give a negative test for atranorin undoubtedly do contain this substance since the GA*o*-T slides became bright yellow, and atranorin should be considered a constant component of this species. Atranorin was not determinable by chromatography in the presence of microphyllinic acid by the methods used in this study because a decomposition product of microphyllinic acid has the same R_f value as atranorin. Microphyllinic acid was proven by its crystals in the GE solution and in 10 percent NaOH solution as well as by chromatography.

REPRESENTATIVE SPECIMENS EXAMINED:

JAPAN: HOKKAIDO: Prov. Ishikari: Mt. Ashibetsu, *Asahina*, 1935 (TNS, 2 collections).

HONSHU: Togakushi, *Faurie* 777, 795 (PC, 2 collections). Towada, *Faurie* 14300, 14304 (PC, 2 collections). Prov. Echigo: Iwafune-gun, Takanosu, *Togashi*, 1959 (TNS). Prov. Hitachi: Tsukuba, *Asahina*, 1924 (TNS). Prov. Inaba: Yazu-gun, Mt. Misumi, *Ikoma* 2512 (TNS). Prov. Iwashiro: Makukawa Hot Spring, *Kurokawa* 58127 (TNS, US). Prov. Kai: Mt. Fuji, Yoshida-guchi, *Hisauchi*, 1928 (TNS). Prov. Kii: Mt. Koya, *Asahina & Togashi*, 1957 (TNS); the same, *Numajiri*, 1926 (TNS, 3 collections). Prov. Kotsuke: Mt. Akagi, *Yasuda* (W). Prov. Mikawa: Mt. Horaiji, Park Iwagoya, *Asahina et al.*, 1960 (TNS). Prov. Musashi:

Mine-no-Yakushi, *Asahina*, 1939 (TNS); Chichibu, Mt. Ryogami, *Kurokawa* 550571 (TNS). Prov. Rikuchu: Mt. Hayachine, Monma-guchi, *Kurokawa* 59275 (TNS). Prov. Sagami: Hakone, Mt. Futago, *Asahina*, 1952 (TNS); Motohakone, *Asahina*, 1924 (TNS). Prov. Settsu: Mt. Myoken, *Ui*, 1935 (TNS). Prov. Shinano: Mt. Yatsu-ga-take, *Kurokawa* 51196, 51197, 51198 (TNS); Pass Kitazawa, Hattyo-zaka, *Asahina*, 1937 (TNS); Mt. Nyugasa, Yoshioka, 1937 (TNS). Prov. Suruga: Mt. Fuji, Omiyama-guchi, 3–2-gome, *Togashi*, 1961 (TNS); Fujiyama, *Faurie* 519 (PC). Prov. Tanba: Minamikuwata-gun, Sogabe-mura, *Togashi*, 1956 (TNS). Prov. Wakasa: Mt. Aoba, *Togashi*, 1956 (TNS, 2 collections). Prov. Yamato: Omine-san, Mt. Sanjo-ga-take, *Togashi*, 1952 (TNS).

SHIKOKU: Prov. Awa: Mt. Ken-zan, *Fujikawa*, 1934 (TNS). Prov. Tosa: Between Mt. Tsutsujo and Mt. Tebako, *Iwatsuki* 1804 (TNS).

KYUSHU: Prov. Bungo: Mt. Urahiko, *Komura*, 1951 (TNS). Prov. Buzen: Mt. Hikosan, *Komura* 984 (TNS). Prov. Higo: Mt. Ichibusa, *Fujikawa*, 1933 (TNS). Prov. Hizen: Mt. Unzen, Nodake, *Asahina & Togashi*, 1958 (TNS). Yakushima, Kosugidani, *Omura*, 1950 (TNS).

KOREA: Prov. Kei-nan: Mt. Chi-san, *Sato* 331a (MSC).

FORMOSA: Prov. Ilan: Piyanan Pass, 1,100–1,300 m., *Kurokawa* 741 (TNS).

SABAH (BORNEO): Kinabalu National Park, from Mesilau River to Kundason, along Mesilau Trail, *Hale* 29269 (US).

JAVA: Res. Pasoeroean, Goenoeng Ardjoena, Tretes-Lalidjiwa-track, *Du Rietz* 95:16 (UPSV).

10. Cetrelia nuda (Hue) Culb. & Culb., comb. nov. PLATE 18

Platysma collatum f. *nudum* Hue, Nouv. Arch. Mus., IV, 1:208. 1899. Type: Japan, Fujiyama, *Faurie* 569 (PC, lectotype).

Cetraria collata f. *nuda* (Hue) Zahlbr., Catal. Lich. Univ. 6:285. 1930.

Parmelia yunnana Hue f. *subnuda* Zahlbr., Hedwigia 74:210. 1934. Type: China, Lidjiang Snow Range, 11,300–12,000 ft., *Rock*, 1931 (W, holotype).

Thallus large, 16–24 cm. broad; lobes 0.6–1.8 cm. broad. Upper surface grayish or ashy-white, smooth, pseudocyphellate, the pores large, conspicuous, irregular, becoming confluent, the largest aggregates exceeding 1 mm. Lower surface black, the margins of some lobes similar in color to the upper surface, wrinkled in part and, if very rugose, with puncta on the crests of the folds. Upper cortex 16–31μ thick; medulla 130–186μ thick; lower cortex 16–22μ thick. Apothecia very common, submarginal to superficial, perforate, irregular at maturity, 1.3–1.5 cm. broad. Spores 8, ovoid, 14–16$\times$6–10μ. Pycnidia always present, large, often pruinose, marginal or at times superficial; conidia 1$\times$5–7μ, rod-shaped, the ends slightly inflated.

MEDULLARY REACTIONS.—K−, C−, KC+ pink, PD−.

CONSTITUENTS.—Alectoronic and α-collatolic acids and atranorin.

DISTRIBUTION (Map, Figure 17).—Widely distributed in the islands Honshu, Shikoku, and Kyushu in Japan and the high mountains of Formosa and Yunnan; locally common on tree trunks and over boulders.

In Japan this species is often conspicuous because of its broad lobes speckled with aggregate pseudocyphellae and its large thallus. The negative reaction of the medulla with C will distinguish it from *Cetrelia*

davidiana and *C. sanguinea*; from *C. collata*, which contains imbricaric acid, the only certain identification is based upon the microchemical demonstration of the alectoronic and/or α-collatolic acids of *C. nuda*. *Cetrelia alaskana* and *C. delavayana*, which may superficially resemble *C. nuda*, differ chemically in producing imbricaric acid and morphologically in having tiny pseudocyphellae rather than large, aggregate ones. Some specimens of *C. braunsiana* with poorly developed isidia may resemble *C. nuda*, but they have very small pseudocyphellae.

This taxon has been recognized in Japan as *Cetraria collata* f. *nuda* (Hue) Zahlbr., and its taxonomy has been confused with that of *Cetrelia chicitae* (the "*Cetraria collata* f. *isidiata*" of the Japanese literature). The reasons for recognizing these three variations as species are discussed in the treatment of *Cetrelia braunsiana* (see p. 495).

Cetrelia nuda is the only species in the genus for which any information on the physiological ecology is available. Hosokawa and his coworkers (1964) reported that in this lichen, called *Cetraria collata* f. *nuda* in their paper, apparent photosynthesis increases both with increasing light and increasing relative humidity, the maximum photosynthesis as measured by carbon dioxide uptake being at 50,000 Lux and 90 percent relative humidity. They believe that these results correlate well with their observation that in closed forests *Cetrelia nuda* occurs primarily in the crowns as opposed to the trunks or the bases of the trees. Cryptogams habitually more abundant at lower levels in the same study sites, they showed, have maximum rates of photosynthesis at much lower light intensities—for example, at about 10,000 Lux for the moss *Thuidium cymbifolium* Doz. & Molk., an inhabitant of the tree base. Furthermore, at high light intensities, *C. nuda* carries on appreciable photosynthesis even when the relative humidity is reduced to 70 to 80 percent. These data would seem to indicate that *C. nuda* has very high light requirements and yet is also at least somewhat adapted to effective photosynthesis at the lower relative humidities that are encountered in places of high illumination.

CHEMICAL ANALYSIS.—All 22 samples of this species tested contained atranorin and alectoronic acid. Twenty of the samples tested also contained α-collatolic acid. Crystals of atranorin were observed in the GA*o*-T solution and sometimes in the GE solution. The substance was also demonstrated chromatographically. Alectoronic acid and α-collatolic acid in mixture were detected by chromatography after observing the crystals in the GE and GAW solutions. Many samples were also checked with 10 percent NaOH to verify the absence of microphyllinic acid.

NOMENCLATURE.—Hue considered this to be a forma of *Platysma collatum*, which he believed to be a sorediate species.

REPRESENTATIVE SPECIMENS EXAMINED:

JAPAN: HONSHU: Onikobe, *Faurie* 283 (PC). Togakushi, *Faurie* 777 (*pro parte*) (PC, 2 specimens). Prov. Aki: Yamagata-gun, Furuyashiki-Mt. Osorerankan, *Kotake*, 1956 (TNS). Prov. Izu: Mt. Amagi, *Asahina*, 1927 (TNS). Prov. Kai: Pass Syosen, *Kurokawa* 521285 (TNS). Prov. Kii: Mt. Koya, *Numajiri* 699 (TNS). Prov. Kozuke: Mt. Akagi, *Asahina*, 1935 (TNS). Prov. Musashi: Chichibu, Mt. Ryogami, *Kurokawa* 550572 (LD, TNS); Nippara, Pass Sengen, *Asahina* 71a (TNS); Mt. Shiroiwa, *Kurokawa* 50380B, 50431B, 510274 (TNS). Prov. Mutsu: Kise, *Murai*, 1933 (TNS). Prov. Sagami: Hakone, Owaku-dani, *Watanabe*, 1955 (TNS). Prov. Shimotsuke: Nikko, *Faurie* 577 (PC); Nikko, Yumoto, *Asahina*, 1952 (TNS). Prov. Shinano: Shibunoyu, Mt. Yatugatake, *Kurokawa* 58197 (MSC). Prov. Suruga: Fujiyama, *Faurie* 508 (*pro parte*), 569 (PC); Mt. Fuji, Omiya-guchi, 2-gome, *Asahina*, 1925, 1926, 1932, 1934 (TNS, 7 collections); Mt. Fuji, Umagayeshi, *Almquist*, 1879 (S). Prov. Yamato: Mt. Omine, Yosigayado, 1,600 m., *Tagawa* 269 (TNS).

SHIKOKU: Prov. Awa: Mt. Ken-zan, *Togashi*, 1956 (TNS). Prov. Iyo: Kitauwa-gun, Mt. Nametoko, *Ogata*, 1928, 1930 (TNS, 2 collections). Prov. Tosa: Mt. Tsutsujo-Mt. Tebako, *Iwatsuki* 1787, 1806, 1811 (TNS).

KYUSHU: Prov. Bungo: Mt. Kuro-dake, *Omura*, 1950 (TNS). Prov. Buzen: Shimoge-gun, Mt. Ura-hiko, *Omura*, 1951 (TNS). Prov. Higo: Mt. Ichibusa, *Fujikawa*, 1933 (TNS).

FORMOSA: Mt. Ali, 2,200 m., *Kurokawa* 13, 37 (TNS); Mt.Tsu-Tson-San, Mt. Ali, 2,300–2,900 m., *Kurokawa* 122 (TNS).

CHINA: YUNNAN: Kou-toui, above Mo-so-yn, 3,000 m., *Delavay*, 1887 (PC); Schweli-Salween–Scheidegebirge, 25°45′N, 2,000–2,800 m., *Gebauer*, 1914 (WU); Mekong-Salween–Scheidegebirge, 26°10′N, *Gebauer*, 1914 (W; WU, 2 collections).

11. Cetrelia olivetorum (Nyl.) Culb. & Culb., comb. nov. PLATE 18

Parmelia olivetorum Nyl., Not. Sällsk Fauna Fl. Fenn. Förhandl., n. ser. 5:180. 1866. Type: Switzerland, collector unknown, s.d. (H-Herb. Acharius, lectotype).

P. perlata f. (?) *rubescens* Th. Fr., Lich. Scand. 112. 1871. Type: Switzerland, collector unknown, s.d. (H-Herb. Acharius, lectotype).

P. rubescens (Th. Fr.) Vain., Bot. Mag. [Tokyo] 35:47. 1921.

P. cetrarioides var. *rubescens* (Th. Fr.) Du Rietz, Nyt Mag. Naturv. 62:75. 1924.

Pseudoparmelia aradensis Gyeln., Acta Fauna Fl. Univ., ser. 2 Bot. [Bucareşti] 1(5–6):6. 1933. Type: Rumania, Arad, *Kümmerle & Jávorka* (BP, holotype).

Parmelia olivaria f. *subvenosa* Gyeln., Repert. Spec. Nov. Fedde 36:302. 1934. Type: Hungary, prope Budapest, *Timkó* (BP, holotype).

[Not *P. perlata* β *olivaria* Ach., Meth. Lich. 217. 1803.]

[Not *P. perlata* β *olivetorum* Ach., Lichenogr. Univ. 458. 1810.]

Thallus small to medium, 6–14 cm. broad; lobes 0.5–1.8 cm. broad. Upper surface light tan or brownish, smooth, sometimes slightly convex, pseudocyphellate, the pores abundant and very small, rarely exceeding 0.5 mm.; the margins of most lobes with dense, fine soredia. Lower surface black, the margins chestnut brown or colored like the upper surface, rarely punctate; rhizines few, black. Upper cortex 19–31μ thick; medulla 96–239μ thick; lower cortex 16–25μ thick. Apothecia rare (unknown in Asian specimens), 0.1–0.7 cm. broad, not perforate;

hymenium 62–109μ thick; subhymenial layers 62–84μ thick, the proper exciple underlain by a thick layer of algae. Spores ellipsoid, 12–15$\times$ 7–10μ. Pycnidia unknown.

MEDULLARY REACTIONS.—K−, C+ pink or red, PD−.

CONSTITUENTS.—Olivetoric acid and atranorin.

DISTRIBUTION (Map, Figure 7).—Appalachian Mountains and northeastern United States and adjacent Canada; southern Scandinavia to the high mountains of southern Europe; high mountains of southwestern China, Formosa, and Japan; over boulders and on tree trunks.

Although *Cetrelia olivetorum* is very closely related to *C. cetrarioides* and *C. chicitae*, it can almost invariably be distinguished from them by the experienced eye. The sum total of its small, difficult-to-describe yet distinctive traits—the slightly convex lobes, the abundant but extremely minute pseudocyphellae, the extremely fine but abundant marginal soredia, and the total lack of laminal soredia—makes it possible to name most specimens at sight. In the southern Appalachians, where this species can be found growing on the same boulders with *C. chicitae*, it almost invariably shows tinier pseudocyphellae and a slightly different habit than the latter species. Nevertheless, some individuals of *C. chicitae* and *C. olivetorum* are so similar that chemical tests are required for positive identifications. *Cetrelia olivetorum* can be distinguished by its distinctive, pinkish-rose medullary reaction with C due to the presence of olivetoric acid. *Cetrelia cetrarioides* produces perlatolic acid or imbricaric acid and *C. chicitae* produces alectoronic and α-collatolic acids, explaining why neither of the species gives a positive reaction with C.

The lack of information about the precise range of this species is in part due to the fact that it is relatively rare and in part because it has been mistaken for the commoner *Cetrelia cetrarioides*. The species seems to be restricted to regions of relatively cool summers and ample rainfall. In all but the northern part of its range, these conditions are met with only at higher elevations and all the southern stations of the species are in mountains. The species usually grows with bryophytes over shaded boulders or on the trunks of trees in moist forests.

The American range is the most accurate part of the map of the total world distribution (Figure 7). Ahti (1964) made a detailed study of the region between the north shore of Lake Superior and Hudson Bay. He records the species from a single locality a little over 100 miles north of the northernmost locality mapped and notes that the lichen there is "rare." Lynge (1921) records a few localities in southern Norway and Du Rietz (1924) and Hakulinen (1963) attribute it to Finland but without citing precise localities. Records for the southern part of the range in Europe are doubtless nearly accurate, the localities corresponding to the higher mountains there.

Generalizations about the distribution in Asia are impossible, yet it seems significant that very few specimens from Japan are present in herbaria in spite of intensive lichenological collecting in that country. On the other hand, a fairly large number of well developed specimens are known from the high mountains of Yunnan Province, and the species may achieve its maximum abundance in Asia in southwestern China.

The frequency with which *Cetrelia olivetorum* has been found mixed with *C. cetrarioides* in packets in herbaria indicates that these species often grow together in nature and doubtless have a very similar physiological ecology.

CHEMICAL ANALYSIS.—All 19 samples tested contained atranorin and olivetoric acid. Olivetoric acid was readily identified in most samples by its crystals in the GE, GAW, and GA*o*-T solutions. To avoid confusion with anziaic acid, all extracts were also checked chromatographically. Physodic acid, known to occur with olivetoric acid in *Cetraria ciliaris* (C. F. Culberson, 1964), was not found in any of the samples of *Cetrelia olivetorum* tested.

NOMENCLATURE.—The specific epithet *olivetorum* is a variation of the earlier Acharian epithet *olivaria* which alluded to the olive trees in southern Europe from which the (different) plants originally called *olivaria* reputedly came. The present species does not grow in the olive region of Europe and the name is wholly inappropriate. It might be noted, however, that olivetoric acid, the characteristic constituent of the medulla of this species, was extracted for the first time from *Cetrelia olivetorum* and was named for it.

The name *olivetorum* has been a source of considerable confusion inasmuch as Acharius and Nylander both used it at different ranks for different taxa. Acharius (1803) named a broad-lobed *Parmelia* from olive trees *P. perlata β olivaria* Ach. and later, for some reason, referred to the same taxon as *P. perlata β olivetorum* Ach., placing the earlier epithet *olivaria* as a synonym (Acharius, 1810). In 1866 Nylander used the epithet *olivetorum* at the species rank and indicated Acharius as the originator of the name although he used it for a taxon different from the one for which Acharius had coined it.

The appropriate sheet in the Acharian herbarium contains three specimens, the illegitimate varietal name *olivetorum* of Acharius being written closest to one which appears to be *Parmelia reticulata* Tayl., a species which could have been collected on olive trees in Europe although its geographic origin is not given. The medulla of this specimen is C—. Both of the other specimens belong to the species under consideration here; their medullary reaction is C+ red, and the larger specimen is labeled "Helvetia." Since *Cetrelia olivetorum* does not grow in the olive zone of Europe, neither of the two Swiss specimens can be

associated with the Acharian epithets *olivaria* or *olivetorum*. These two specimens, with their distinctive medullary reactions with C, are surely the ones Nylander referred to in his diagnosis of *Parmelia olivetorum*: "Ach. ex hb. ipsius, cui speciei medulla thalli ope hypochloritis calici erythrinice tingitur." The binomial *Parmelia olivetorum* must be attributed to Nylander alone (Art. 72) and typified upon one of the C+ specimens. The larger specimen labeled "Helvetia" is the lectotype. This specimen is also designated as the lectotype of *P. perlata* f. (?) *rubescens*, a taxon described apparently as a forma by Th. Fries who seems to have understood the nomenclatural history of the *olivetorum* names in spite of the solution that he offered by proposing another name altogether.

REPRESENTATIVE SPECIMENS EXAMINED:

U.S.A.: MAINE: Knox Co.: Rockland, *Merrill, Lich. Exs.* 99 (DUKE). York Co.: Kennebunkport, *Pier*, 1917 (UC, DUKE).

NEW HAMPSHIRE: Cheshire Co.: Alstead, *Seymour*, 1921 (UC, DUKE). Grafton Co.: North Woodstock, collector unknown (DUKE).

VERMONT: Caledonia Co.: McIndoe's Falls, *Bliss*, 1918 (DUKE).

NEW YORK: Essex Co.: Wilmington, *Brodo* 499 (DUKE).

PENNSYLVANIA: Monroe Co.: Mt. Pocono, *Kaiser* 1910 (DUKE).

WEST VIRGINIA: Pocahontas Co.: Gaudiner Knob, *Hale, Lich. Amer. Exs.* 56 (UC).

VIRGINIA: Giles Co.: Mountain Lake, *Culberson* 11180, 11238 (DUKE). Madison Co.: Shenandoah National Park, *Hale* 19213 (*pro parte*) (US). Page Co.: Little Stony Man Cliffs, Shenandoah National Park, *Hale* 19219 (US); Skyline Drive, Crescent Rocks, *Hale* 18167 (US).

NORTH CAROLINA: Avery Co.: Near the Avery-Caldwell County line, *Culberson* 11770 (DUKE). Rockbridge Co.: Mile 35, Blue Ridge Parkway, *Hale* 17813 (US).

OHIO: Locality unknown, *Sullivant* (CB).

MICHIGAN: Isle Royale: Rock Harbor, *Harper* 160 (UC, DUKE).

WISCONSIN: Langlade Co.: Langlade, *Culberson* 2007 (DUKE). Price Co.: Park Falls, *Culberson* 1814 (DUKE).

JAPAN: Prov. Echigo: Sasa-ga-mine, *Togashi*, 1950 (DUKE).

FORMOSA: Mt. Ali, Mt. Tsu-Tson-san, 2,300–2,900 m., *Kurokawa* 133 (TNS). Prov. Nantoh, Lisan, *Kurokawa* 880 (TNS).

CHINA: SZECHWAN: Mt. Lose-schan, south of Nengyüen, 3,950 m., *Handel-Mazzetti* 1441 (W).

YUNNAN: Lenago Pass between Mekong and Yangtze, 27°43′ N, *Gebauer*, 1914 (W, WU); Fang-Yang-Tchang, above Mo-To, *Delavay*, 1887 (PC); Long, above Ta-pin-tze, *Delavay*, 1887 (PC); Koua-la-po, *Delavay* 1595 (*pro parte*) (PC); Hee-chan-men, *Delavay*, 1887 (PC); Yen-tze-hay, *Delavay*, 1887 (PC, 2 collections).

NEPAL: Above Sauwala Khola, 10,500 ft., *Stainton et al.* 43796 (*pro parte*) (BM).

RUMANIA: TRANSYLVANIA: Hunyad, *Lojka* (PC); Arad, *Kümmerle & Jávorka*, s.d. (BP).

POLAND: Bieszczady Zachnodnie Mountains, Puszcza Bukowa, Mt. Paportna, 810 m., *Glanc*, as *Tobol.*, *Lichenoth. Polonica* 174 (DUKE).

HUNGARY: Near Budapest, m. Nagyhárshegy, *Timkó* (BP).

SWITZERLAND: Léman, collector unknown (PC).

GERMANY: BAVARIA: München, *Arnold, Lich. Monacensis Exs.* 324a,b, *Arnold, Lich. Monacensis Exs.* 6 (PC).

FRANCE: CÔTES-DU-NORD: Forêt de Lorges, *des Abbayes*, 1929 (Herb. des Abbayes).

FINISTÈRE: Forêt de Cranou, *des Abbayes*, 1933 (Herb. des Abbayes).

HAUTES-PYRÉNÉES: Cauterets, *Lamy de la Chapelle* (PC).

12. Cetrelia pseudolivetorum (Asah.) Culb. & Culb., comb. nov. PLATE 19

Parmelia (*Amphigymnia*) *pseudolivetorum* Asah., Journ. Jap. Bot. 27:16. 1952. Type: Japan, Mt. Fuji, *Asahina* (TNS, holotype).

Thallus small to large, 0.7–18.0 cm. broad; lobes 0.5–1.5 cm. broad. Upper surface grayish or grayish-white or uniformly light brownish or tan in old herbarium specimens, smooth or becoming cracked, pseudocyphellate, the pores small, to 0.5 mm. broad, punctiform or slightly elongate, the margin and occasionally the surface with granular, simple or coralloid isidia, often grading into dorsiventral, dissected lobulae. Lower surface black, the margins brown or colored like the upper surface, not punctate; rhizines few, black. Upper cortex 16–30μ thick; medulla 150–200μ thick; lower cortex 11–17μ thick. Apothecia very rare, 0.4–1.7 cm. broad, mostly perforate; hymenium 53–78μ, hyaline; subhymenial layers 40–53μ thick. Spores 8, ellipsoid, (11—)16–22×9–12μ. Pycnidia unknown.

MEDULLARY REACTIONS.—K—, C+ pink, P—, UV—.

CONSTITUENTS.—Olivetoric acid and atranorin.

DISTRIBUTION (Map, Figure 9).—The mountains of central Japan, Formosa, and Yunnan, China, and the Himalayas; usually on rock or over boulders with bryophytes.

Cetrelia pseudolivetorum has a pink medullary reaction with C due to the presence of olivetoric acid thereby distinguishing it from the two morphologically similar species for which it would most probably be mistaken, *C. japonica* (with microphyllinic acid) and *C. sinensis* (with imbricaric acid). In reality, though, the bulk of the specimens of *C. pseudolivetorum* differ morphologically from these species (see the discussion of *C. japonica*, pp. 511–512).

Some forms of *Cetrelia pseudolivetorum* with isidia or isidioid lobulae instead of the expanded dorsiventral lobulae more typical of the species might be mistaken for the common Japanese species *C. braunsiana*. The latter species has very delicate coralloid isidia and is C— but KC+ because of its production of alectoronic acid. The two species can usually be distinguished without the need of chemical thallus spot tests, however.

Cetrelia pseudolivetorum might also be mistaken for some rare forms of *C. sanguinea* with well-developed lobulae. If it has small marginal isidia, it might be mistaken for *C. isidiata*. Both these species give a red

(rather than a pinkish) medullary reaction with C and both produce anziaic acid rather than the olivetoric acid.

Although chemically identical, *Cetrelia olivetorum* and *C. pseudolivetorum* are morphologically distinct. The margins of *C. olivetorum* have extremely fine, powdery, white soredia while those of *C. pseudolivetorum* have isidioid lobulae or similar outgrowths. There are no integradations between the two species although badly damaged specimens of *C. pseudolivetorum*, in which the delicate marginal appendages have been broken off exposing the white medulla, might be mistaken for *C. olivetorum*.

Cetrelia pseudolivetorum shows considerable variability, but the variation is so continuous that there is no reason to suspect that the population is not sufficiently uniform to be considered a single species. Forms with coralloid marginal isidia recalling those of *C. braunsiana* may be found, while in other extreme variants the marginal outgrowths take the form of the exaggerated, expanded, dorsiventral lobulae of certain forms of *C. japonica* and *C. sinensis*. But all the intergradations are present as well, and these minor variations need not be reflected in the taxonomy.

This species is restricted to the mountains of southern and southeastern Asia and Japan. The elevation data for the known localities indicate a vertical range of about 1,500–3,600 m. with most of the specimens coming from about 2,000–3,000 m. Unfortunately the labels of the specimens give few habitat data, but when a substrate has been noted, it is usually rock. In reality, however, the habitat ecology of this species is probably very similar to that of others in the genus. For example, a particularly rich collection made on shrubs at about 10,500 feet in Nepal by Stainton, Sykes, and Williams consisted of a mixture of *Cetrelia pseudolivetorum*, *C. olivetorum*, *C. braunsiana*, and *C. collata*. Or it might be that distinct ecological races with regard to substrate preference exist in some correlation with the morphological plasticity noted above. Systematic field studies might be expected to elucidate this point.

Chemical analysis.—Thirty-one samples of this species were tested in the same manner as described for *Cetrelia olivetorum*. All contained atranorin and olivetoric acid.

Representative specimens examined:

JAPAN: Prov. Shinano: Lake Shirakaba, *Asahina* 58505 & *Togashi* (DUKE); Mt. Norikuratake, *Asahina* 52805 (TNS). Prov. Shimotsuke: Nikko, Chuzenji, *Nakaji* 2510 (TNS). Prov. Suruga: O-miya-guchi, 1-go-han, Mt. Fuji, *Asahina* 34125 (TNS); Lake Saiko (Nishi-no-umi), near Mt. Fuji, *Culberson* 10078, 10643 (DUKE).

FORMOSA: Mt. Ali, Mt. Tsu-Tson-San, 2,300-2,900 m., *Kurokawa* 121, 134, 137 (TNS). Between Su-Su-Lu and Mt. Ali, 200-2,200 m., *Kurokawa* 611 (TNS). Mt. Nan-Fu-Ta-San, 1,500-2,400 m., *Kurokawa* 928 (TNS). Mt. Shin-Kao-San,

Mt. Shi-San, 3,300-3,600 m., *Kurokawa* 332 (TNS); the same, 3,100-3,300 m., *Kurokawa* 253 (TNS); Pianan to Sunlien, *S. Asahina* 3608 (TNS).

CHINA: Moupin (eastern Tibet). Without precise locality, *David* 1869 (PC, 2 collections).

YUNNAN: Tsang-chan, above Ta-li, 4,000 m., *Delavay*, 1885 (PC, 2 collections); the same, *Delavay*, 1888 (PC, 3 collections); Yen-tze-hay, 300 m., *Delavay*, 1887, (PC); Hee-chan-men, *Delavay*, 1887 (PC); Fang-Yang-Tchang, above Mo-so-yn *Delavay*, 1887 (PC); Lopin-chan Pass, 3,200 m., *Delavay*, 1888 (PC); Lopin-chan Pass, above Lan-Kong, *Delavay*, 1888 (PC, 2 collections); Lopin-chan Pass, *Delavay*, 1888 (PC).

SIKKIM: Wallanchoon, *Hooker* 2087 (K).

INDIA: Chakrata, *Awasthi* 501 (H).

NEPAL: Above Sauwala Khola, 10,500 ft., *Stainton et al.* 4379b (*pro parte*) (BM).

13. Cetrelia sanguinea (Schaer.) Culb. & Culb., comb. nov. PLATE 19

Cetraria sanguinea Schaer. *in* Moritzi, Zoll., Syst. Verz. Java Pflanz. 129. 1845–1846 (1846). Type: Java, Mt. Pangerano, *Zollinger*, 1842–1844 (G, holotype).

Imbricaria sanguinea (Schaer.) Schwend. *in* Naegeli, Beitr. Wiss. Bot. 3:159. 1863.

Platysma sanguineum (Schaer.) Hue, Ann. Jard. Bot. Buitenzorg 17:177. 1901.

Parmelia megaleia Nyl., Synops. Lich. 1:378. 1860. Type: Java, *Junghuhn* (PC, lectotype).

Platysma megaleium (Nyl.) Nyl., Flora 52:290. 1869.

Imbricaria megaleia (Nyl.) Jatta, Nuov. Giorn. Bot. Ital., n. ser. 9:469. 1902.

Platysma subperlatum Nyl., Flora 49:130. 1866. Type: Java, Togoe, *Kurz*, 1861 (H-Herb. Nylander, lectotype).

Aspidelia wattii Stirt., Trans. & Proc. New Zealand Inst. 32:82. 1899 (1900). Type: Himalayas, *Watt* 7070 (BM). (Invalidly published; cf. Culberson, 1966a).

Thallus medium to large, 11–24 cm. broad; lobes 0.5–1.5 cm. broad. Upper surface whitish or tan, brownish in old herbarium specimens, sometimes brownish or blackish toward the margins, smooth to minutely wrinkled, pseudocyphellate, the pores small, rarely more than 0.5 mm. broad and often inconspicuous or even lacking altogether on some lobes, the margins of the lobes entire to sometimes minutely lacerate or beset with lobulae. Lower surface jet-black, the margins often dark brown, not punctate; rhizines few, black. Upper cortex 16–25μ thick, impregnated with a noncrystalline brown pigment; medulla 93–170μ thick; lower cortex 16–28μ thick. Apothecia frequent, very large, perforate, cup-shaped when young, irregularly expanded and radially lacerate with maturity, 1.5–4.2 cm. broad, the thalloid exciple densely pseudocyphellate; hymenium 60–93μ thick; subhymenial layers 43–61μ thick, impregnated with a yellow pigment turning reddish brown with $FeCl_3$. Spores 8, 17–22$\times$9–14μ, the spore wall about 2μ thick. Pycnidia large, marginal; conidia 1$\times$4μ, rod-shaped.

MEDULLARY REACTIONS.—K−, C+ bright red, PD—.

CONSTITUENTS.—Anziaic acid and atranorin.

DISTRIBUTION (Map, Figure 15).—In the high mountains of Japan, southwestern China, Java, and Sumatra; on the bark of trees and shrubs.

While *Cetrelia sanguinea* resembles a number of other species in habit, the one for which it might most easily be mistaken is *C. davidiana*, the only closely related C+ species. In *C. davidiana*, however, the reaction produces a pink coloration instead of the red one characteristic of *C. sanguinea* and reflects the presence of olivetoric acid rather than anziaic acid. Of course, microchemical or chromatographic analyses are required for a precise determination of the substance responsible for positive reactions with C and critical taxonomic identifications here should not be made without them.

A single Japanese collection containing anziaic acid closely resembles many of the plants of *Cetrelia sanguinea* from Java where the species has been the most extensively collected. It lacks apothecia and has marginal lobulae somewhat resembling those of *C. japonica*. A chemical study of the many specimens referred to *C. japonica* in herbaria upon the basis of gross morphology alone might well extend the known Japanese range of *C. sanguinea*.

In restricted areas within its range the species may be very common. For example, there are many specimens in herbaria from Mt. Pangerango, the type locality, where collections of the species have repeatedly been made incidental to other explorations, an apparent testimony to the abundance and conspicuousness of the lichen there. From labels giving elevation data, the species in the East Indies seems to be found between 1,400 and 3,800 m., most of the specimens coming from about 3,000 m. The Japanese specimen is also from a mountain locality.

CHEMICAL ANALYSIS.—The species is very uniform in the lichen substances produced. Of the 67 specimens tested microchemically, all produced atranorin and anziaic acid. Atranorin was usually observed in the GA*o*-T solution, and the absence of the colorless needles formed by olivetoric acid in this solution was noted. Some samples also showed atranorin in the GE solution. Anziaic acid usually crystallized from the GAW solution, but less often also from the GE solution. All extracts were chromatographed to verify the presence of atranorin and anziaic acid. The crystals of anziaic acid in the GAW solution were quite variable, but no additional compounds were suspected on the basis of the chromatographic results.

The apothecia of this species may contain a yellow pigment (not usnic acid) which was not identified.

The generic name *Aspidelia* Stirt., under which Stirton included the description of a species based upon a specimen referable to *C. sanguinea* (see synonymy above), was published without a generic description

and is thus invalid and cannot be taken up for *Cetrelia* or for any other genus (Culberson, 1966a).

ADDITIONAL SPECIMENS EXAMINED:

JAPAN: HONSHU: Mt. Osore-san, *Sato*, 1935 (H).
JAVA: Mt. Pangerango, 3,000 m., *Möller*, 1897 (LD, S); the same, *Poch*, 1906 (WU); the same, 2,500 m., *Schiffner* 3007 (M); the same, 3,050 m., *Hochreutiner* 936 (G); Mt. Gede, *Karsten*, s.d. (TUR); the same, 2,400 m., *Hochreutiner* 876 (G); Tjibodas, Mt. Gede, 1,400 m., *Palmer & Bryant* 822 (US); Mt. Ardjoeno, 3,800 m., *Groenhart* 160 (H); Res. Pasoeroean, Goenoeng Ardjoena, track from Lalidzina to Ardjoeno-top, *Du Rietz* 18a:1, 18a:2, 24:4, 51:3 (UPSV); the same, Lalidjina-Welirang-track, *Du Rietz* 54:3, 60:3, 60:4, 60:5, (UPSV); the same, Tretes-Lalidjina-track, *Du Rietz* 95:7, 95:17a, 95:17b, 99:1 (UPSV); and the same, *Skottsberg* 1929 (UPSV, 14 collections).
SUMATRA: Mt. Singalang, 2,500 m., *Schiffner* 3441 (W, WU).
CHINA: YUNNAN: Mekong-Salween-Scheidegebirge, *Gebauer*, 1914 (W).
PAKISTAN(?): Himalayas, Lingalelah Range, 12,000 ft., *Watt* 7070 (BM).

14. Cetrelia sinensis Culb. & Culb., sp. nov. PLATE 20

Thallus maximus, 17–26 cm. latus; laciniae 1–2 cm. latae, marginibus dense instructae vel planta tota saepe cristata lobulis palmatis vel subpal natis, vel angustis et isidioideis, vel expansis et foliosis. Superficies superior aequaliter pallide cinerea (albida apud plantas vivas?), levis, pseudocyphellata, pseudocyphello punctato vel nonnihil elongato parvae (ca. 0.5 mm. latae). Superficies inferior picea, marginibus ad extremos lacinianum pallida, non punctata; rhizinae nigrae. Cortex superior 19–28μ crassus, subprosoplectenchymatosus, strato corticali summo ferrungineo-colorato, medulla 140-183μ crassa; cortex inferior 16–22μ crassus. Apothecia ignota. Pycnidia magna, nigra, in marginibus laciniarum; conidia 1.5$\times$6μ, recta.

Thallus large to very large, 17–26 cm. broad; lobes 1–2 cm. broad, the margins densely fringed with palmately or subpalmately divided lobulae, narrow and isidioid or more broadly expanded and lobelike, so dense that the specimens may appear cristate. Upper surface uniformly light brown (perhaps grayish-white when fresh), smooth, pseudocyphellate, the pores punctiform or somewhat elongate, very small (ca. 0.5 mm. broad). Lower surface jet-black, a marginal zone near the tips of the lobes colored like the upper surface, apparently not punctate; rhizines black. Upper cortex 19–28μ thick, subprosoplectenchymatous and essentially pseudoparenchymatous, the upper part of the cortex suffused with a brownish, noncrystalline pigment; medulla 140–183μ thick; lower cortex 16–22μ thick, prosplectenchymatous. Apothecia unknown. Pycnidia large, black, restricted to the marginal lobulae; conidia 1.5 $\times$ 6μ, rod-shaped.

TYPE.—"Sur les pierres dans les bois aux sources du Lan-Kien-ho, près du col Hee-chan-men," Yunnan, China, *Delavay* 30 (PC, holotype).

MEDULLARY REACTIONS.—K−, C−, KC−, PD−.

CONSTITUENTS.—Imbricaric acid and atranorin.

DISTRIBUTION (Map, Figure 18).—High mountains of Yunnan, China, and Formosa; over boulders (and on trees?), apparently very rare.

Since this species is known from only two collections, it is not possible to assess its morphological variability. It appears, however, that it may not be different morphologically from *Cetrelia japonica*, which contains microphyllinic acid. *Cetrelia sinensis* must be identified by the presence of imbricaric acid. See the discussion for *Cetrelia japonica* (p. 511) for a further discussion of morphologically similar species and their distinguishing characteristics.

CHEMICAL ANALYSIS.—The six known specimens (from two collections) of the species were tested and all contained imbricaric acid and atranorin. Hydrolysis of the residues from two samples and chromatography of the products show a faint spot at a position corresponding to olivetol-2-carboxylic acid. It may or may not be due to the presence of perlatolic acid.

ADDITIONAL SPECIMENS EXAMINED:

FORMOSA: Mt. Shin-Kao-San, Mt. Shi-San, 3,300–3,600 m., *Kurokawa* 449 (TNS).

CHINA: YUNNAN: Lan-Kien-ho near Hee-Chan-men, *Delavay* 30 (PC).

Platismatia Culb. et Culb., gen. nov.

Thallus 5–18(–23) cm. latus; laciniae (0.1–)0.3–2.2(–2.5) cm. latae. Superficies superior pallide cinerea vel citrella, viridiolivacea, vel apud exemplaria vetera herbarii aequaliter obscure citrella, saepe rugosa, pseudocyphellata vel isidiata sed raro sorediata. Superficies inferior nigra, rhizinata, saepe punctata. Cortex superior (15)18–28(32)μ crassus, prosoplectenchymatosus; medulla (30–)65–210(–280)μ crassa, alba; cortex inferior (10–)13–28(–30)μ crassus. Apothecia (0.1–)0.4–1.5(–4.0) cm. lata, marginalia vel submarginalia, vulgo perforata; hymenium (34–)39–70(–125)μ crassum; asci IKI+ caerulescentes; strata subhymenialia (13–)18–50(–78)μ crassa, IKI+ caerulescentia, viridicaerulescentia, lavendulina, vel purpurea, subtus fere sine algis. Sporae 8-nae, parvae, ellipsoideae vel subglobosae, (3.5–)5–8(–10) $\times$3 5μ. Pycnidia marginalia, immersa, saepe deficientia; conidia rara, 1$\times$5(–7)μ, recta, extremis non inflatis. Typus generis *P. glauca* est.

Thallus 5–18(–23) cm. broad; lobes (0.1–)0.3–2.2(–2.5) cm. broad. Upper surface ashy-white, tan, or greenish-brown (uniformly dull tan

in old herbarium specimens), often rugose, pseudocyphellate in some species, isidiate in some species, rarely sorediate. Lower surface black, with few rhizines, punctate in some species. Upper cortex (15–)18–28 (–32)μ thick; medulla (30–)65–210(–280)μ thick; lower cortex (10–) 13–28(–30)μ thick. Apothecia (0.1–)0.4–1.5(–4.0) cm. broad, marginal or submarginal, commonly perforate; hymenium (34–)39–70(–125)μ, the asci IKI+ blue; subhymenial layers (13–)18–50(–78)μ thick, IKI+ blue, blue-green, lavender, or purple, usually without underlying algae. Spores 8, small ellipsoid or subglobose, (3.5)5–8(–10)$\times$ 3–5μ. Pycnidia marginal, immersed, often absent; conidia rare, 5–(7)$\times$ 1μ, rod-shaped, the ends not inflated.

CONSTITUENTS.—Atranorin and caperatic acid; fumarprotocetraric acid in one species.

Certain authors have referred some members of the *Cetraria glauca* group, which constitutes the genus *Platismatia*, to the genus *Platisma* (sometimes written as the orthographic variant "*Platysma*"). *Platisma* as a generic name has probably been associated primarily with the species *Cetraria glauca* more than with any other species, at least in the minds of most lichenologists, and we hoped that it could be used for the *Cetraria glauca* group essentially in the sense that Dahl (1952) had proposed earlier. The genus had not been typified, however, and when an exhaustive nomenclatural study of the *Platisma* names was made (Santesson and Culberson, 1966), it was impossible to typify any of them in such a way that they could be used for this or any other group of plants. The new generic name *Platismatia* is a madeup derivative from the old name *Platisma*.

Artificial Key to the Species of *Platismatia*

1. Thallus isidiate or sorediate.
   2. Upper surface or margins of lobes isidiate or sorediose-isidiate.
      3. Some lobes becoming narrow, coralloid, fruticose appendages of the normally foliose thallus; upper surface not pseudocyphellate; lower surface not punctate.
         4. Lobes of the foliose part of the thallus expanded, commonly more than 5 mm. wide; broadly distributed . . . . . **3. P. glauca** (some forms)
         4. Lobes of the foliose part of the thallus narrow, strap-shaped, less than 5 mm. wide; northwestern North America . . **4. P. herrei** (rare forms)
      3. All the lobes broadly foliose, none becoming coralloid or fruticose; upper surface pseudocyphellate; lower surface punctate or not.
         5. Upper surface with prominent, vertical, reticulate ridges, the isidia confined primarily to the crests of the ridges; thallus IKI−; lower surface not punctate; North America and Europe . . . . **7. P. norvegica**
   5. Upper surface without prominent reticulate ridges but often with poorly defined, interrupted ones; thallus IKI− or IKI+; lower surface punctate or not.
      6. Upper surface pseudocyphellate, IKI− or IKI+; lower surface punctate or not; isidia rarely on the margins of the lobes; Asia.

7. Pseudocyphellae minute, inconspicuous, usually confined to the crests of the thallus ridges; thallus surface IKI−; lower surface usually punctate; mountains of southern Asia and Japan. **1. P. erosa**

7. Pseudocyphellae large and conspicuous, round to elliptical, scattered; thallus surface IKI+; lower surface not punctate; Japan. **5. P. interrupta**

6. Upper surface not pseudocyphellate, IKI+; lower surface not punctate; isidia commonly on the margins of the lobes; America or Europe.

8. Lobes broadly foliose, not strap-shaped, commonly more than 5 mm. wide; widely distributed . . . . . **3. P. glauca** (some forms)

8. Lobes narrow and strap-shaped, less than 5 mm. wide; northwestern North America . . . . . **4. P. herrei**

2. Upper surface sorediate, not isidiate.

9. Upper surface conspicuously pseudocyphellate; Japan. **5. P. interrupta** (some forms)

9. Upper surface not pseudocyphellate; widely distributed but absent from Japan . . . . . **3. P. glauca** (some forms)

1. Thallus neither isidiate nor sorediate.

10. Upper surface with sharply defined, continuous, reticulate ridges, not pseudocyphellate; medulla of American plants PD+ orange-red.

11. Medulla PD−; lower surface punctate; Formosa . . **2. P. formosana**

11. Medulla PD+ orange-red; lower surface not punctate; northwestern North America . . . . . **6. P. lacunosa**

10. Thallus without sharply defined reticulate ridges but often with inconspicuous, interrupted ridges and folds or thallus pitting, pseudocyphellate or not; medulla PD−.

12. Upper surface pseudocyphellate; apothecia unknown; Asia.

13. Pseudocyphellae large and conspicuous; upper surface not commonly blackened; lower surface not punctate; Japan . . **5. P. interrupta**

13. Pseudocyphellae small; upper surface or margins commonly darkened or mottled with black; lower surface punctate; Asia.

14. Thallus surface reticulately lined, the pseudocyphellae associated with the lines; mountains of southern Asia and Japan. **1. P. erosa** (nonisidiate forms)

14. Thallus surface without conspicuous lines; the margins of some lobes blackening conspicuously; Sabah (Borneo) . . . **8. P. regenerans**

12. Upper surface not pseudocyphellate; apothecia common; North America.

15. Lobes narrow and strap-shaped, rarely reaching 5 mm. broad; western North America . . . . . **9. P. stenophylla**

15. Lobes broadly expanded, usually exceeding 5 mm. broad; eastern North America . . . . . **10. P. tuckermanii**

1. Platismatia erosa Culb. & Culb. sp. nov. PLATE 20

Cetraria formosana var. *isidiata* Zahlbr., Repert. Spec. Nov. Fedde 33:60. 1934. Type: Mt. Niitaka (=Mt. Morrison), Formosa, *Sasaki* (W, holotype).

Thallus mediocris, ad 11–12 cm. latus; laciniae 0.5–2 cm. latae. Superficies superior sordide citrella vel pallide grisea, marginibus laciniarum olivacea, reticulata, reticulo, saepe nigrescente; isidiata, isidiis fere raris, brevibus, pinquibus, simplicibus et in reticulo positis sed coralloideis, in marginibus laciniarum. Superficies inferior punctata, picea,

marginibus fusca vel pallida; rhizinae paucae, simplices vel fasciculatae, nigrae, solum in partibus vetustioribus thalli. Cortex superior 22–26 (–28)μ crassus; medulla 50–90(–114)μ crassa, IKI—; cortex inferior 16–21(–26)μ crassus. Apothecia rarissima, ad 7 mm. lata, submarginalia, perforata; hymenium 39–47μ crassum; asci IKI+ intense caerulescentes; strata subhymenialia 21–29μ crassa, IKI+ lavendula; sporae 8-nae, ellipsoideae, 3–4$\times$5–8μ. Pycnidia ignota.

Thallus medium, to 11–12 cm. broad, loosely attached; lobes 0.5–2 cm. broad, broadly rounded. Upper surface light tan or ashy-gray, tinged with brown at the margins of the lobes, broadly reticulately ridged and veined, the crests of the ridges often darkening, and pseudocyphellate with minute pores and often bearing isidial scars resembling pseudocyphellae; isidiate, the isidia usually infrequent, short, stout, or simple and usually confined to the ridges or thallus cracks but becoming coralloid and well developed at the margins of the lobes in some specimens. Lower surface punctate, jet-black, the marginal zone light brown or tan; rhizines few, simple or fasciculate, black, confined to the older parts of the thallus. Upper cortex 22–26(–28)μ thick; medulla 50–90(–114)μ thick, IKI—; lower cortex 16–21(–26)μ thick. Apothecia very infrequent, to 7 mm. broad, submarginal, perforate; hymenium 39–47μ thick, the asci IKI+ dark blue; subhymenium 21–29μ thick, IKI+ lavender, without underlying algae; spores 8, ellipsoid, 3–4$\times$5–8μ. Pycnidia unknown.

Type.—Yatsu-ga-take, Mount Kitayoko-dake, Province of Shinano, Japan, *Kurokawa* 58349 (TNS, holotype).

Medullary reactions.—K—, C—, KC—, PD—.

Constituents.—Caperatic acid, atranorin, and an unidentified yellow pigment.

Distribution (Map, Figure 30).—Mountains of Honshu, Japan, Formosa, Philippines, Java, Vietnam, Sikkim, and Nepal; on tree trunks.

Platismatia erosa is distinguished by the broadly "eroded" reticulation of its upper surface, the pseudocyphellae and isidial scars associated with the thallus ridges, and the puncta on the lower surface.

In Japan some specimens of *Platismatia erosa* have previously been referred to *Cetraria formosana* as var. *isidiata*, but the plants differ from *P. formosana* in a number of ways. The thallus folds and ridges, sharp and conspicuous in *P. formosana*, are less distinct in *P. erosa*. *Platismatia formosana* never has isidia, and *P. erosa* is typically isidiate, although rarely richly so, and some fragmentary or poorly developed specimens may lack isidia altogether. The crests of the thallus ridges in *P. erosa* always bear at least a few pores. While most of these pores are doubtless pseudocyphellae, some of them seem to be scars where

isidia have broken off. Holes in the upper cortex such as these, regardless of their origin, are unknown in *P. formosana*.

Platismatia erosa also superficially resembles *P. norvegica* although their ranges do not overlap anywhere. It differs from *P. norvegica* in having pseudocyphellae on the upper thallus surface and puncta on the lower surface while the latter species never produces these pores. Although reticulate on the upper surface, *P. erosa* lacks the delicate yet sharp and continuous network that ornaments the surface of *P. norvegica*. The species also differ in many minor characteristics such as the morphology of the isidia. The isidia of *P. erosa* are short and very coarse and usually simple while those of *P. norvegica* are slender, delicate, and often coralloid.

Platismatia erosa as it is represented in Japan and in the high mountains of the mainland of southern Asia is a very clearly defined species of conservative variation. Since most of the specimens seen in this study were from these regions, a few somewhat different-looking plants from the Philippines and Java are assigned to this species with reluctance and qualification. The anomalous southern plants differ in their habit by a number of subtle, hard-to-describe ways from those of the main part of the distribution to the north. They have larger and more abundant pseudocyphellae on the upper surface, fewer puncta on the lower surface, more richly developed isidia, and less well defined thallus ridges and reticulations. These southern plants (especially the Javanese ones) when considered together, however, seem to be quite uniform. Perhaps they belong to a distinct taxon.

Some individuals of *Platismatia erosa*, and especially the atypical southern specimens provisionally referred to this species, may also superficially resemble *P. regenerans* from Sabah. The latter species, however, has no isidia, and it has pseudocyphellae which are larger and more conspicuous than those of typical *P. erosa*. It also lacks the ridging seen in *P. erosa*, and its upper surface is entirely smooth.

CHEMICAL ANALYSIS.—Of the 17 samples tested, nine were extracted directly with acetone. The residues from these extracts all showed caperatic acid in both the GE solution (two crystal forms) and the GAW solution, and atranorin in the GE and GA*o*-T solutions. Residues from eight samples extracted with cold benzene showed atranorin in the GE and GA*o*-T solutions (Plate 2, Figure 7) but no protolichesterinic acid in the GE solution. The residue from a subsequent acetone extract gave the characteristic crystal forms of caperatic acid in the GE solution (Plate 3, Figure 18) and in the GAW solution (Plate 2, Figure 11). In addition to atranorin and caperatic acid, nine samples showed yellow crystals in the GE solution (Plate 6, Figure 35) which may be due to an unidentified yellow pigment. Some residues containing the yellow pigment also showed clusters of fine yellowish-tan nee-

dles (Plate 6, Figure 36) in the GA*o*-T solution. The same combination of yellow crystals in the GE solution and fine needles in the GA*o*-T solution was observed in preparations from some samples of *Platismatia interrupta*, *P. formosana*, and *P. regenerans*, suggesting that the same substance or combination of two substances occurs in these species as well.

ADDITIONAL SPECIMENS EXAMINED:

JAPAN: HONSHU: Prov. Kai: Mt. Kobushi, 2,000 m., *Asahina*, 1933 (TNS, 3 collections). Prov. Shinano: Mt. Tadeshina, *Kurokawa* 510038 (TNS); Yatsu-ga-take, Mt. Tengu, *Kurokawa* 58240 (TNS, US); Yatsu-ga-take, Takami-ishi, *Kurokawa* 58301 (TNS); Yatsu-ga-take, Mt. Kitayoko-dake, *Kurokawa* 58349 (TNS); Yatsu-ga-dake, Mt. Naka-no-dake, *Togashi & Kurokawa* (TNS). Prov. Musashi: Mt. Kobushi, Pass Karisaka, *Kurokawa* 521018 (TNS).

FORMOSA: Mt. Niitaka, *Sasaki*, 1927 (W).

PHILIPPINES: MOUNTAIN PROV.: Mt. Data, Barrio, *Hale* 26301, 26751 (US); the same, Heald Logging Area 9, *Hale* 26082, 26105 (US).

JAVA: Res. Pasoeroean, Goenoeng Ardjoena, Lalidjina-Welirang-track, *Du Rietz* 61:2, 61b:2, 62:1, 65:3, 68:1 (UPSV); the same, track from Lalidjina to Ardjoeno top, *Du Rietz* 36:1 (UPSV).

VIETNAM: Langbian Mountains near Dalat, 1,800 m., *Tixier*, 1962 (DUKE).

CHINA: YÜLINGKONG: Gomba La, 3,700 m., *Smith* 14062 (UPS).

SIKKIM: No locality, *Thomson* (H-Herb. Nyl., K, M); no locality, *Thomson*, 289 (G,M). East Himalayas, 8,500 ft., *Awasthi* 354 (H).

NEPAL: East Nepal, Mewakhola Valley, 11,000–11,500 ft., *Awasthi* 2292 (UPS); Khumbu, 3,900–4,000 m., *Poelt* L36, L37 (M).

2. Platismatia formosana (Zahlbr.) Culb. & Culb., comb. nov. PLATE 25

Cetraria formosana Zahlbr., Repert. Spec. Nov. Fedde 33:59. 1933–1934 (1934). Type: Formosa, Mt. Arisan, *Asahina* F.89 [not "84" as in the original citation]. (W, holotype).

Thallus small to medium, 5–19 cm. broad; lobes 0.3–2.5 cm. broad. Upper surface ashy-white or gray (uniformly brown in old herbarium specimens), abruptly interrupted with broad reticulate ridges up to 1 mm. high at right angles to the surface, not pseudocyphellate. Lower surface black toward the center, but large zones, especially toward the margin, chestnut-brown, punctate, the entire lower surface covered with abundant, tiny pores; rhizines few, black, simple or compound-fasciculate. Upper cortex 19–31μ thick; medulla 29–102μ thick between the ridges, IKI—; lower cortex 10–25μ thick. Apothecia infrequent, submarginal, perforate, 1.5–4.0 mm. in diameter; hymenium 39–47μ thick; subhymenial layers 18–26μ., without underlying algae. Spores 8, small, ellipsoid, 5–7×3–4μ. Pycnidia marginal, immersed, only the ostiole visible; conidia 1×5–7μ, rod-shaped, the ends not inflated.

MEDULLARY REACTIONS.—K—, C—, KC—, P—.

CONSTITUENTS.—Caperatic acid, atranorin, and an unidentified yellow pigment.

DISTRIBUTION (Map, Figure 28).—Mountains of Formosa.

The thallus of *Platismatia formosana* has a broad and severe reticulation that is particularly striking. The long, continuous ridges are composed of both cortex and medulla and may be as high as 2 mm. with perfectly vertical sides and without correspondingly deep depressions in the lower surface of the thallus. The sharpness of the ridges is striking in comparison to the worn, more gentle ridges of *P. erosa*, although the overall pattern of ridging of the thallus surface is highly similar and the species are obviously very closely related.

Platismatia formosana might be compared with *P. lacunosa*, but their patterns of thallus ridging are quite different. In *P. formosana* the spaces between the broadly separated, vertical ridges are flat while in *P. lacunosa* the sloping ridges are separated by U-shaped valleys. The two species can be separated immediately by their medullary reactions with *p*-phenylenediamine: *P. formosana* is negative while *P. lacunosa* is brick-red due to the presence of fumarprotocetraric acid.

The species is known only from the mountains of Formosa and earlier records for it from Japan (Sato, 1943) are doubtless all referable to *Platismatia erosa*.

CHEMICAL ANALYSIS.—Two samples were tested and both showed atranorin and caperatic acid. Both crystal forms of caperatic acid were observed in the GE recrystallization of the acetone extract. Both samples also showed a yellow pigment (not usnic acid) soluble in warm benzene and recrystallizing from the GE solution. The crystals in this solution resemble those from *P. erosa* (Plate 6, Figure 35), and one sample also gave the clusters of fine needles in the GA*o*-T solution that seemed to be the same as those associated with the occurrence of the yellow pigment in *P. erosa* and *P. interrupta* (Plate 6, Figure 36). The same yellow pigment may also occur in *P. regenerans*.

ADDITIONAL SPECIMENS EXAMINED:

FORMOSA: Mt. Arisan, Numanodaira, above 7,000 ft., *Asahina* F.89 (W); Mt. Niitaka (=Mt. Morrison), *Sasaki*, 1927 (W), *Suzuki*, 1935 (H); the same, Hattsu-kan, *Suzuki*, 1935 (TNS, 3 collections); Mt. Daibu, *Yasuda* 448 (H).

3. Platismatia glauca (L.) Culb. & Culb., comb. nov. PLATE 21

Lichen glaucus L., Sp.Pl.1148. 1753. Type: Europe, Linnean Herbarium Sheet 1273–139 (LINN, lectotype).

Cetraria glauca (L.) Ach., Method. Lich. 296. 1803.

C. glauca var. *chilensis* Räs., Ann. Bot. Zool.-Bot. Fenn. Vanamo 20(3):4. 1955. Type: Chile, Prov. Chiloé, Petrohué, *Hosseus* 167 (M, isotype).

Lobaria glauca (L.) Hoffm., Deutschl. Fl. oder Bot. Taschenb., Theil für das Jahr 1795, Cryptogamie. 149. 1795 (1796).

Parmelia glauca (L.) Hepp, Lichenen-Fl. Würzburg. 23. 1824.

Physcia glauca (L.) DC. *in* Lam. & DC., Fl. Franç., ed. 3, 2:401. 1805.

Platysma glaucum (L.) Frege, Deutschl. Bot. Taschenb., 2. Theil für das Jahr 1812. 167. 1812. [Not seen.]

Thallus medium, 8–15 cm. broad; lobes 0.3–2.0 cm. broad, the margins with soredia, simple or coralloid isidia, or both, or branched and divided into fruticose lobes, which in turn may be sorediate or isidiate or both. Upper surface whitish or whitish-green or tinged with yellow or, especially in South American specimens, very distinctly yellow, often with darkened areas, smooth to strongly reticulately wrinkled, not pseudocyphellate, smooth or with coralloid or sorediose isidia in discrete patches or diffusely scattered. Lower surface jet-black, the margins brown, colored like the upper surface or white, smooth or reticulately wrinkled and pitted, not punctate; rhizines few to many, simple or compound, brown or black. Upper cortex 16–26μ thick, prosoplectenchymatous; medulla white, 62–155(–200)μ thick, IKI+ lavender; lower cortex 16–25μ thick, prosoplectenchymatous. Apothecia very rare, 0.5–1.0 cm. broad, marginal, perforate or not; hymenium 34–56μ thick, the asci IKI+ blue or blue-green; subhymenial layer 16–52μ thick, IKI+ lavender or bright purple, not underlain by algae; spores 8, small, ellipsoid to ovoid, 3.5–8.5×3–5μ. Pycnidia not seen. (See the taxonomic discussion below.)

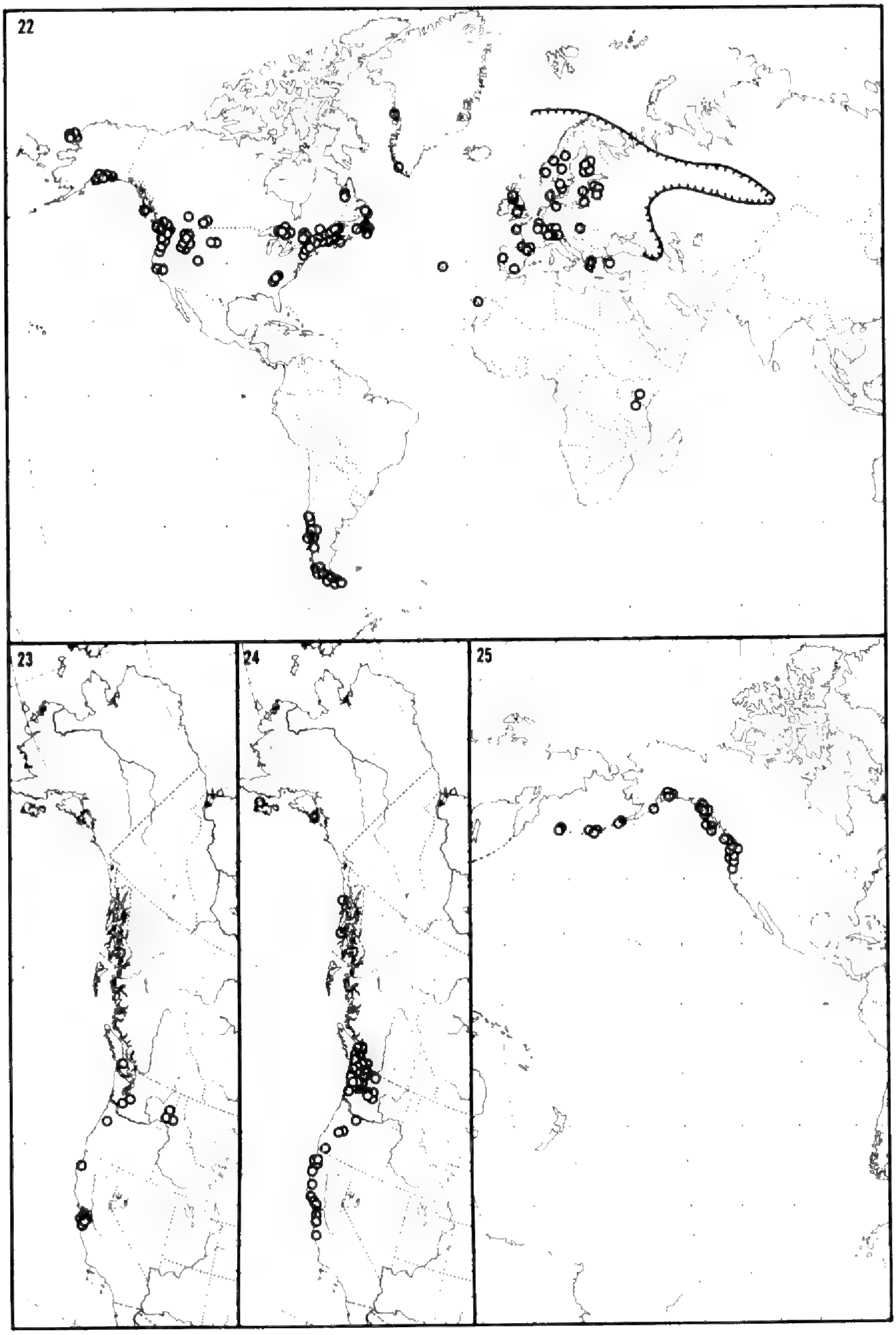
MEDULLARY REACTIONS.—K−, C−, KC−, PD−.

CONSTITUENTS.—Caperatic acid and atranorin.

DISTRIBUTION (Map, Figure 22).—Southern Greenland, northeastern and northwestern North America and coastal Alaska, Patagonia, central Asia (U.S.S.R.) west through all of Europe, the Canary Islands and the Azores, and in the high mountains of Kenya and Tanzania; on tree trunks and on rocks and boulders.

No other species treated in this monograph has a broader range of morphological variation than *Platismatia glauca*. There is a bewildering range of forms from plants with lobes bearing soredia to sorediose isidia to coralloid isidia to isidioid fruticose branches. All these traits, however, intergrade, and all possible combinations of characters can be found in the herbarium, although certainly not at every locality in the field where the species occurs. If only the extremes of the variations were seen, it would be unbelievable that all the forms constituted a single species. In spite of the plastic morphology of this species, far fewer infraspecific taxa of it have been described than one might expect, considering the taxonomic tradition in Europe. All this reflects, we believe, a general recognition by lichenologists of the innate continuity of the variation in this doubtless very ancient species.

When a large series of specimens is examined or when the species is studied in the field, one is tempted to see distinct local races. For example, the eastern North American populations seem to have a somewhat shiny thallus surface as compared to that of the western North American populations which seem to be much duller. These apparent differences, however, could not be associated with any con-



FIGURES 22–25. Distributions. 22. *Platismatia glauca* (L.) Culb. & Culb. 23. *P. stenophylla* (Tuck.) Culb. & Culb. 24. *P. herrei* (Imsh.) Culb. & Culb. 25. *P. lacunosa* (Ach.) Culb. & Culb.

stant or demonstrable structural or chemical differences. Similarly, the South American plants in general look more distinctly yellow than those from the Northern Hemisphere. No chemical explanation for this color difference could be found.

In the present study no pycnidia of this species were seen. Hillmann and Grummann (1957), however, note in the description of this species in their flora of Brandenburg: "Pykniden selten, randständig, braun oder schwärzlich. Pyknokonidien gerade, an einem Ende verdickt, 6–7 × 0.8–1.0μ."

It is not surprising that the species showing the greatest morphological variation of all those treated here should also have the broadest geographic range. *Platismatia glauca* is a boreal to temperate species, but it is conspicuously absent from eastern Asia where it is replaced by other members of the genus, notably *P. interrupta* and *P. erosa*. In Africa it is known with certainty only from Mt. Aberdare in Kenya and Mt. Kilimanjaro in Tanzania, although Flagey (1896) cites it from the Atlas Mountains of North Africa. These localities, moreover, are the only certain African stations for any species of "*Cetraria*" in the broad sense.

The map of the total range of *Platismatia glauca* (Figure 22) is only approximate. Too few Soviet specimens with adequate geographic information were seen to allow the construction of a meaningful map for eastern Europe and central Asia. The outlined eastern part of the range of the species in the Old World is based on a map published by Rassadina (1950) in her careful study of *Cetraria* in the U.S.S.R. Since there are no differences in the taxonomy of *P. glauca* at the species level between her treatment and ours, we have used directly the information that she gives. Also, in the range as indicated for western North America, the real distribution may actually extend a bit farther north than we have mapped it.

Although *Platismatia glauca* is widely distributed, it is rare in large parts of its range, for example in the southern parts of its distribution in North America. In Europe the species is doubtless by far most common in the milder western parts and in the British Isles.

Chemical analysis.—Eleven samples from throughout the range of the species were tested and all contained caperatic acid but no protolichesterinic acid. The cold benzene extract showed atranorin in the GE and GA*o*-T solutions but no recognizable fatty acid in the GE or GAW solutions. The subsequent acetone extract contained caperatic acid (GE, GAW, and GA*o*-T). Tests in the GE solution gave mixed crystal forms of caperatic acid (Plate 3, Figures 14 and 16). The acetone extracts were also chromatographed in pyridine-ethyl acetate-water (1:2:1) and sprayed with a stable PD solution, but no PD+ compounds other than atranorin were detected.

NOMENCLATURE.—The oldest specific epithet for this polymorphic, widely distributed lichen is *Lichen glaucus*, from Linnaeus' *Species Plantarum* (1753). There are, however, several other old specific epithets that also refer to *Cetraria glauca* (L.) Ach. sens. lat.: *Lichen fallax* Web. (Spicilegium Florae Goettingensis. 244. 1778), *Lichen fraudulentus* Gmel. (in L., Syst. Nat., ed. 13, 2 [2]:1371. 1791), and *Lichen membranaceus* Lam. (Encycl. Méthod., Bot. 3: 492. 1789 [1791–1792]). Zahlbruckner (1930) lists nomenclatural synonyms of all these basionyms. None of these old names has been typified in the present study because none is required for the present taxonomic treatment. In the event that a future interpretation recognizes more than one species, it will be necessary to determine the precise reference through typification of these names before assigning specific epithets to segregates of *Platismatia glauca* sens. lat.

In addition to the above names, the epithet *Lichen ampullaceus* L. (Sp. Pl. 1146. 1753) has traditionally been assumed to refer to *Platismatia glauca*. There is no specimen bearing the epithet *ampullaceus* in the Linnean Herbarium. From the original description ("Lichen foliaceus planiusculus lobatus crenatus, peltis globosis inflatis"), however, the name has often been interpreted to refer to monstrous forms of *P. glauca* infected by parasitic fungi (cf. Santesson and Culberson, 1966). If so, the name can be rejected as based upon a monstrosity.

REPRESENTATIVE SPECIMENS EXAMINED:

GREENLAND: JULIANEHAAB DISTRICT: Uperniviarssuk, *Dahl*, 1937 (US); Qagssiarssuk, *Dahl*, 1937 (US).

MIQUELON ISLAND: Locality unknown, *Delamare*, s.d. (COLO).

CANADA: LABRADOR: Bottle Harbor, *Waghorne*, 1882 (US).

NEWFOUNDLAND: St. John, *Fries*, 1871 (S); Codroy Valley, Oregans, *Hall* 34, 35, 36, 41 (WIS).

QUEBEC: Gaspé-Est: Bonaventure Island, off Percé, *Imshaug* 26501 (MSC), *Shushan* S23026 (COLO). Montmorency: Laurentides National Park, Lac Jacques Cartier, *Imshaug* 26336 (MSC). Matane Co.: Mont Blanc, *Frère Fabius*, 1953 (DUKE, 4 collections). Frontenac Co.: Mont Megantic, Masson 6068 (WIS).

NOVA SCOTIA: Chester, *Greenwood* 1558 (COLO–ABS).

NEW BRUNSWICK: Albert Co.: Fundy National Park, Herring Cove, *Imshaug* 26532, 26585 (MSC).

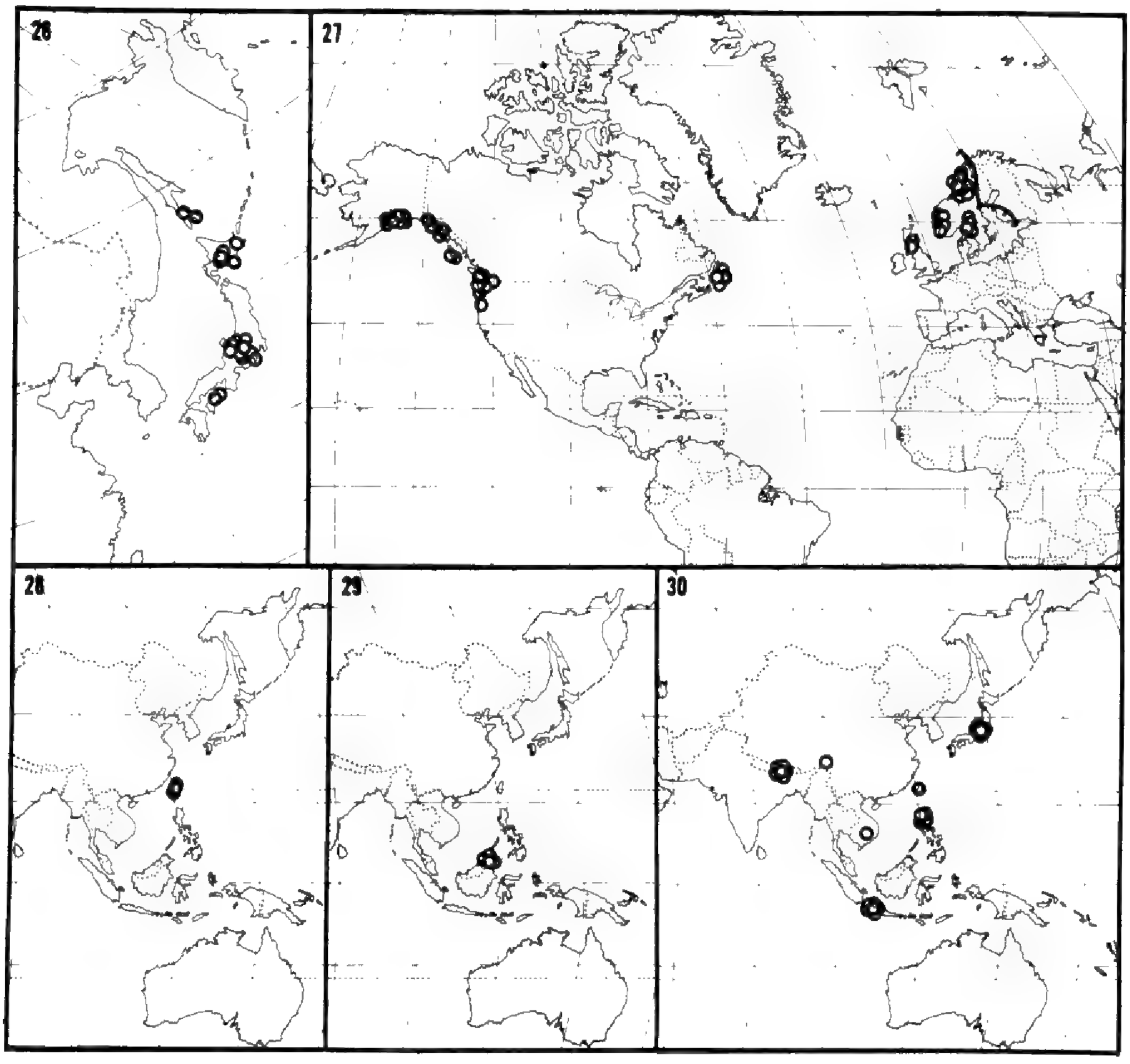
ONTARIO: Groundhog River, west of Timmins, *Wetmore* 6247 (COLO, MSC, US).

SASKATCHEWAN: Cypress Hills, *Lamb* 6133 (DUKE, WIS).

ALBERTA: Banff National Park, Johnson Creek, *Weber* S23560 (COLO).

BRITISH COLUMBIA: Queen Charlotte Islands: Graham Island, *Persson* (COLO). Vancouver Island: Locality unknown, *Lyall*, 1858–1859 (US, 2 collections); Comox, *Macoun* 88 (CAL, MSC, US, WIS).

U.S.A.: MAINE: Hancock Co.: Mt. Desert Island, *Davis* 21, 46 (US). Knox Co.: Camden, *Merrill, Lich. Exs.* 139 (US). Piscataquis Co.: Mt. Katahdin, *Degelius*, 1939 (US). Washington Co.: Cutler, *Davis* 14g (US); North Lubec, *Cummings, Decades North Amer. Lich.* 279 (MSC, US).



FIGURES 26–30. Distributions. 26. *Platismatia interrupta* Culb. & Culb. 27. *P. norvegica* (Lynge) Culb. & Culb. 28. *P. formosana* (Zahlbr.) Culb. & Culb. 29. *P. regenerans* Culb. & Culb. 30. *P. erosa* Culb. & Culb.

NEW HAMPSHIRE: Coos Co.: Mt. Washington, *Llano*, 1941 (WIS). Grafton Co.: Mt. Lafayette, *Kaiser* 64 (COLO–ABS).

VERMONT: Lamoille Co.: Mt. Mansfield, *Cain* 25549 (COLO), *Merrill* 1922 (DUKE).

MASSACHUSETTS: Berkshire Co.: Mt. Greylock, *Imshaug* 24095 (MSC).

NEW YORK: Ulster Co.: Cornell Mountain, *Imshaug* 24062 (COLO, MSC).

TENNESSEE: Sevier Co.: Mt. Le Conte, *Degelius*, 1939 (US, 2 collections).

NORTH CAROLINA: Avery Co.: Roan Mountain, *Hale* 18086 (US).

MICHIGAN: Keeweenaw Co.: Isle Royale National Park, *Wetmore* 2509 (COLO, DUKE, MSC).

MINNESOTA: Cook Co.: Susie Islands *Thomson* 4023 (WIS).

SOUTH DAKOTA: Lawrence Co.: Benchmark, *Wetmore* 8503 (MSC).

MONTANA: Flathead Co.: Glacier National Park, Fish Lake, *Imshaug* 7287 (WIS). Missoula Co.: South of Missoula, *Stickney* PFS–573 (WIS). Sanders Co.: South of Thompson Falls, Dry Creek, *Stickney* 1005, 1005a, 1005b (WIS).

WYOMING: Crook Co.: Taylor Divide Road, *Wetmore* 9824 (MSC).

COLORADO: Boulder Co.: Bull Gulch, *Erdman*, as *Weber, Lich. Exs.* 4 (COLO, DUKE, MSC, WIS).

ALASKA: Prince William Sound, Thum Bay, Knight Island, *Eyerdam* 254, 282, 284 (CAL). Washington Bay, Kuiu Island, *Eyerdam* 1080, 1086, 1142 (COLO). Kenai Peninsula, Seward, *Hultén*, 1932 (UPS); Admiralty Island, Windfall Harbor, *Stephens* 243 (CAL).

WASHINGTON: Clark Co.: 5 mi. east of Vancouver, *Pechanec* S4717 (COLO). Island Co.: Langley, *Grant*, 1923 (WIS, 2 collections). Jefferson Co.: Olympic Rain Forest, *Howard* 4317 (WTU). King Co.: Red Mountain, *Eyerdam* 1557 (COLO, WTU). Lewis Co.: Tenina, *Frye* (COLO–ABS). Pierce Co.: Mt. Rainier National Park, White River, *Imshaug* 391 (US, WIS). Snohomish Co.: Marysville, *Grant*, 1929 (CAL, US). Spokane Co.: North of Spangle, *Cooke* 23203 (COLO-ABS, WIS). Stevens Co.: Springdale, *Cooke* 23237 (WIS). Thurston Co.: Olympia, *Becking* 5203462d (WTU). Whatcom Co.: Maple Mead Farm, *Herre*, 1949 (WIS). Whiteman Co.: Kamiak Butte, *Imshaug* 16446 (MSC).

OREGON: Benton Co.: Corvallis, *E. J. K.*, 1921 (WIS). Hood River Co.: Cloud Gap, *Hale* 21558 (DUKE). Jackson Co.: Medford, *Darrow* 233 (WIS). Lane Co.: Oakridge, *Howard* 4713 (WTU). Union Co.: Mill Creek, *Sheldon* 9010 (US).

IDAHO: Bonner Co.: Sandpoint, *Knox* S15842, S15844 (COLO). Idaho Co.: Nez Perce National Forest, *Cooke* 20694, 20708 (WIS). Nez Perce Co.: Clearwater Canyon, *Cooke* 22910, 22918 (WIS). Lattah Co.: St. Joe, *Herre* 7457 (COLO, WIS). Lewis Co.: Winchester, *Cooke* 25107 (WIS).

CALIFORNIA: Siskiyou Co.: Locality unknown, *Herre*, 1942 (WIS). Sonoma Co.: Santa Rosa, *Baker*, 1897 (UC).

CHILE: MALLECO: Pidir-Nalmel, *Sparre* 5092 (S); Angol, *Dusén*, 1896 (UPS).

CAUTÍN: Volcán Llaima, *Sparre* 4826 (S).

VALDIVIA: Lago Panguipulli, *Santesson* 3943 (UPS); Lago Riñihue, Enco, *Santesson* 7249, 7273, 3607 (UPS).

AYSÉN: Coyhaique, *Santesson* 4397, 4453, 4484 (UPS); Puerto Aysén, *Santesson* 4323.

CHILOÉ: Petrohué, *Hosseus* 167 (M).

MAGALLANES: Isla Riesco, *Santesson* 2084, 9011a, 8198 (UPS); Lago del Toro (Maravilla), *Santesson* 6330, 6505 (UPS); Tierra del Fuego, Canal Whiteside, Puerto Yartou, *Santesson, Lich. Austroamer.* 469b (LD, MSC, UPS); Canal Beagle, *Santesson* 7445 (UPS); Isla Hoste, *Santesson* 1333 (UPS); Punta Arenas, *Santesson* 5116 (UPS).

ARGENTINA: Río NEGRO: Lake Nahuel Huapí, *Lamb* 5834 (UPS); Lago Frias, *Lamb* 5984 (UPS).

TIERRA DEL FUEGO: Lago Fagnano, *Santesson* 1583 (UPS); Ushuaia, *Dusén* 247 (UPS), *Dusén*, 1896 (GB, S, UPS), *Santesson* 433, 1215 (UPS), *Skottsberg*, 1902 (S, 3 collections), *Santesson, Lich. Austroamer.* 469a (LD, MSC, UPS); Sierra Alvear, *Santesson* 706 (UPS).

NORWAY: HORDALAND: Granvin, *Havaas*, 1910 (DUKE).

SÖRTRÖNDELAG: Leinstrand, *Hoëg*, as *Magn., Lich. Sel. Scand. Exs.* 260 (GB, S).

SWEDEN: DALARNE: Lima, *Hasselrot* (S).

JÄMTLAND: Åre, *Hasselrot* (S).

SMÅLAND: Bunn, *Santesson*, 1932 (S).

VÄSTERGÖTLAND: Koläby, Trädet, *Vrang, Krypt. Exs. Vindobon.* 2763 (MSC, UC).

VÄRMLAND: N. Ny, *Hasselrot*, 1938 (S).

FINLAND: ETELÄ-HÄME: Lammi, *Ulvinen*, 1960 (UC).

POHJOIS-KARJALA: Keitele, Vuonamo, *Huuskonen*, 1960 (UC).

U.S.S.R.: ESTONIA: Eesti, Kedder, *Wasmuth*, 1910 (H); Distr. Keila, Vääna, *Pärn*, 1960 (DUKE); Tallin-Pääskula, *Pärn*, 1960 (DUKE); Insula Saaremaa, *Sünnaa*, s.d. (DUKE).

LITHUANIA: Peninsula Kura, *Trass*, 1959 (DUKE).
SIBERIA: Sajangebirge, *Plotnikov*, 1927 (DUKE).
TURKEY: Mt. Ida, *Cyrén*, 1933 (S).
SCOTLAND: INVERNESS-SHIRE: Moidart Peninsula, Shiel Bridge, *Culberson & Culberson* 11827 (DUKE).
ARGYLLSHIRE: Ardnamurchan Peninsula, Kilchoan, *Culberson & Culberson* 11586 (DUKE).
WALES: BRECONSHIRE: Hay-on-Wye, *Culberson & Culberson* 11859 (DUKE).
CAENARVONSHIRE: Gwynant Lake, *Culberson & Culberson* 11926 (DUKE).
RADNORSHIRE: Penybont, *Culberson & Culberson* 11851 (DUKE).
DENMARK: JYLLAND: River Gudenna, Borre Forest, *Leth*, 1870 (UC).
GERMANY: SCHLESWIG-HOLSTEIN: Schleswig, *Saxen*, 1957 (DUKE).
BREISGAU: Freiburg, *Lösch*, as *Arn., Lich. Exs.* 1723 (PC).
HOLLAND: GELDERLAND: Bermekon, *Maas Geesteranus* 2480 (S).
CZECHOSLOVAKIA: Banska Stiavnica, Finkova, *Suza, Lich. Bohemoslov* 56 (DUKE).
GREECE: THESSALIA: Mt. Olympos, *Szatala*, as *Kofaragó-Gyeln., Lichenoth.* 193 (BM).
PELOPONNESOS: Messina, *Degelius*, 1955 (GB).
FRANCE: ARDENNES: Montherme, *Culberson & Culberson* 10530 (DUKE).
FINISTÈRE: Roc Trévezel, *Culberson & Culberson* 10503 (DUKE).
HAUTE-GARONNE: Lac d'Oô, *Culberson & Culberson* 11895 (DUKE).
HAUTES-PYRÉNÉES: Cauterets, *Jeanjean* 7771 (DUKE); Pont d'Espagne, *Culberson & Culberson* 11713 (DUKE).
VOSGES: Schiessrothried, *Werner*, 1959 (MSC, 2 collections).
SPAIN: JAÉN: Sierra de Cazola, *Degelius*, 1952 (S).
PORTUGAL: BEIRA ALTA: Serra da Estrela, *Tavares*, 1946 (S).
CANARY ISLANDS: Palma, *Pitard*, 1883, 1886, 1906 (DUKE, 3 collections); the same, *Bornmuller* (W).
AZORES: Pico, *Persson*, 1937 (UPS, 2 collections).
KENYA: Mt. Aberdare, *Fries & Fries*, 1922 (UPS).
TANZANIA: Kilimanjaro, above Marangu, 3,225 m., *Hedberg* 1374e (UPS).

4. Platismatia herrei (Imsh.) Culb. & Culb., comb. nov. PLATE 22

Cetraria herrei Imsh., Bryologist 57:6. 1954. Based on *C. glauca* b. *stenophylla*.
Cetraria glauca b. *stenophylla* Tuck., Synops. No. Amer. Lich. 1:36. 1882. Type: U.S.A., Oregon, *Hall*, 1871 (FH, lectotype).
Cetraria tuckermanii Herre, Proc. Washington Acad. Sci. 7:340. 1906. (Not Oakes *in* Tuck., 1843). Based on *C. glauca* b. *stenophylla*.

Thallus medium, 9–12 cm. broad; lobes linear, narrow, 0.5–4 mm. broad, sometimes much broader (up to 8 mm.) near the base. Upper surface whitish or pale, smooth to very minutely pitted or wrinkled, not pseudocyphellate or sorediate, isidiate, the isidia simple to branched and coralloid, densely fringing the margins, rarely on the upper surface. Lower surface white or pale with conspicuous, discrete, well delimited, jet-black or dark brown zones, especially in the older parts; rhizines black, rare, a few at the places of attachment only. Upper cortex 21–26μ thick, medulla 91–177μ thick, the hyphae oriented parallel to the axis of the lobe, IKI+ lavender; lower cortex 15–26(–31)μ thick, prosoplectenchymatous. Apothecia not common, 3–8 mm. broad, ter-

minal, imperforate; hymenium 47–65μ thick; subhymenium 13–18μ thick. Spores 8, ellipsoid or spheroid, 4–5 $\times$ 5–8μ. Pycnidia few, black, minute, marginal; conidia 1$\times$5μ, rod-shaped.

MEDULLARY REACTIONS.—K−, C−, KC−, P−, UV−.

CONSTITUENTS.—Caperatic acid and atranorin.

DISTRIBUTION (Map, Figure 24).—Extreme western North America from southern Alaska south to central California; on the bark of trees.

Platismatia herrei is one of the most beautiful and intricately formed species in the genus. It can be distinguished from all other members of the genus by the delicate but conspicuous isidia fringing the edges of the linear lobes. In some specimens there are fruticose coralloid structures on the margin identical to (but invariably smaller than) those seen in some forms of *P. glauca*. Occasional specimens of *P. herrei*, indeed, show the typically narrow, linear lobes arising from much broader basal ones making one wonder if the plants called *P. herrei* might represent only a localized western race of *P. glauca*. But although some specimens may superficially give this impression, the distinctively narrow lobes, the characteristically delicate marginal corolloid isidia, and the black mottling in conspicuous discrete patches of the undersurface are so different from the traits of the typical race of *Platismatia glauca* inhabiting the Pacific Northwest that the distinctness of the species is beyond doubt.

Platismatia herrei is an excellent example of a North American endemic species with an extreme Pacific coastal distribution. Its range is almost identical in extent to the coastal portion of the distribution of western hemlock, *Tsuga heterophylla* (Raf.) Sarg.

CHEMICAL ANALYSIS.—Five samples of this species were tested. The benzene extracts showed atranorin in the GE and GA*o*-T solutions and by chromatography. No fatty acids were observed in these extracts, but the subsequent acetone extracts showed caperatic acid in the GE, GAW, and GA*o*-T solutions. Tests for atranorin in the GA*o*-T solution showed two types of yellow crystals—one typical of atranorin and the other smaller and more sharply curved.

ADDITIONAL SPECIMENS EXAMINED:

U.S.A.: ALASKA: Hecla Island, *Foster*, 1913 (COLO). Prince William Sound, Knight Island, Thum Bay, *Eyerdam* 305 (WIS). Washington Bay, Kuiu Island, *Eyerdam* 428 (COLO). Kodiak Group, Raspberry Island, Port Vita, *Eyerdam* 390 (WIS).

WASHINGTON: Clallam Co.: Swan Bay, Ozette Lake, *Brown & Muenscher* 143 (UC, US); West Fork, Twin Rivers, *Eyerdam* 3162 (COLO); Sequin, *Grant* 41 (COLO-ABS); Olympic Mountains, *Grant* 3001 (COLO-ABS). Jefferson Co.: Port Discovery, *Brown & Muenscher* 142 (UC, US). Pierce Co.: Mt. Rainier National Park, Van Trump Trail, *Howard* 4202 (COLO, WTU); the same, White River, *Imshaug* 414, 434 (US); the same, Tahoma Creek, *Imshaug* 1741 (US); the same, Eagle Peak Trail, *Imshaug* 1563 (US). Snohomish Co.: Mt. Pilchuck, *Larrison*,

1947 (WIS); Marysville, *Grant*, s.d. (COLO). Whatcom Co.: Mt. Baker, 2,000 ft., *Herre* 3234 (COLO-ABS).

OREGON: Locality unknown, *Hall*, 1871 (FH). Josephine Co.: Between Cave Junction and O'Brien, *Weber* 8044 (COLO). Lane Co.: Florence, *Marr*, 1941 (COLO); Eugene, collector unknown, 1936 (COLO).

CALIFORNIA: Locality unknown, *Bolander* 28 (FH). Humboldt Co.: Eureka, *Howe, Lich. Boreali-Amer.* 143 (WIS), the same, *Howe*, as *Cummings et al., Decades of North Amer. Lich.* 213 (DUKE, MSC, US, WIS); Pepperwood, *Tavares* 361 & *Seear* (UC). Jackson Co.: Highway 227, *Tavares* 111d & *Chisaki* (UC). Marin Co.: Mt. Tamalpais, *Schneider*, 1903 (UC); Tomales Bay, *Mann & Bolander* 31 (UC); Inverness, *Tavares* 564 (UC). Mendocino Co.: South fork of Eel River below Elder Creek, 1,000 ft., *Tavares & Sharsmith*, 1961 (UC). Monterey Co.: Locality unknown, *Booth*, 1878 (FH). Santa Cruz Co.: Boulder Creek, 700 ft., *Hasse* 3051 (UC). Sonoma Co.: Gualala, *McMillan* 110 (UC); 24 mi. south of Gualala, *Seear & Tavares* 318c (UC).

CANADA: BRITISH COLUMBIA: Islands, Gulf of Georgia, *Hill* (COLO-ABS); Mayan Island, *Hill*, 1904 (COLO-ABS); Queen Charlotte Islands, Moresby Island, head of Bigsley Inlet, *Persson* 14 (COLO); Thurlow Island, *Dawson*, 1885 (H); Victoria, Mt. Douglas, *Kverno* S1987 (COLO, US); Vancouver Island, *Lyall*, 1858–1859 (US, WIS), *Macoun* 16 (US); the same, Port Renfrew, *Herre*, s.d. (UC); the same, Nanaimo, *Macoun* 97 (UC, MSC, US, WIS), *Krajina et al.* 3729 (DUKE).

5. Platismatia interrupta Culb. & Culb., sp. nov. PLATE 22

Thallus parvus vel mediocris, 6–12 cm. latus; laciniae 0.3–2.0 cm. latae. Superficies superior grisea (sordide citrella apud exemplaria vetera herbarii) vel marginibus pallide fusca, levis vel reticulis interruptis indistincte rugosa, pseudocyphellata, pseudocyphellis conspicuis, rotundis, elongatis vel confluentibus, granulose-sorediatis vel subisidiatis. Superficies inferior picea, marginibus castanea vel albida, non punctata; rhizinae paucae, nigrae. Cortex superior 18–26μ crassus, prosoplectenchymatosus; medulla 65–104μ crassa, IKI− vel IKI+ dilute violacea; cortex inferior 13–21μ crassus. Apothecia et pycnidia ignota.

Thallus small to medium, 6–12 cm. broad; lobes 0.3–2.0 cm. broad. Upper surface gray (uniformly light in old herbarium specimens) or tinged with light brown on the margins, smooth to very obscurely wrinkled with a discontinuous reticulation, pseudocyphellate, the pores conspicuous, round to irregular, elongate or confluent, becoming coarsely sorediate or isidioid in some specimens. Lower surface jet-black at the center, a marginal zone up to 2 cm. broad chestnut brown or conspicuously white (or light brown in old specimens), not punctate; rhizines very few, black. Upper cortex 18–26μ thick, prosoplectenchymatous, with minute brownish crystals, IKI− or IKI+ very pale lavender; medulla white, 65–104μ thick; lower cortex prosoplectenchymatous, 13–21μ thick, crystals absent or, if present, only a few in the light-colored zone. Apothecia and pycnidia unknown.

TYPE.—Mount Norikura, Shinano Province, Japan, *Asahina*, 1952 (TNS, holotype).

MEDULLARY REACTIONS.—K−, C−, KC−, PD−.

CONSTITUENTS.—Caperatic acid, atranorin, and an unidentified yellow pigment.

DISTRIBUTION (Map, Figure 26).—Sakhalin Island and Japan, especially in the mountains; very common on tree trunks and over boulders.

Platismatia interrupta is very common in Japan and is, in fact, one of the most abundant of all the macrolichens there. It is obviously the Far Eastern equivalent of *P. glauca*, a species that is exceedingly common in large areas of the Northern Hemisphere but which is apparently absent from the extreme Orient altogether.

Platismatia interrupta differs from P. *glauca* in having pseudocyphellae on the upper surface of the lobes and an indistinct and discontinuous reticulation of the upper surface that reminds one of a further, almost complete breakdown of the reticulate ornamentation of the upper surface of *P. erosa*. In addition, the upper surface of *P. interrupta* is IKI−, or nearly so, while it is blue in *P. glauca*.

The only Japanese species for which the common *Platismatia interrupta* might be mistaken is the rare *P. erosa*. The upper surface of *P. interrupta* is not pseudocyphellate in the same manner as *P. erosa*, and the habit of the reticulation is different. The pseudocyphellae in *P. interrupta* are large, conspicuous, and generally distributed, but they are small, inconspicuous, and confined to the crests of the ridges in *P. erosa*.

Some especially isidiate individuals of *P. interrupta* may resemble *P. norvegica*. *Platismatia norvegica* has much more prominent reticulate ridging and lacks the conspicuous pseudocyphellae characteristic of *P. interrupta*.

One specimen with pseudocyphellae typical of *P. interrupta* but with essentially strap-shaped lobes with marginal isidia was seen from Sakhalin Island (Aikawa, *Asahina*, 1932, TNS). With the exception of the pseudocyphellae, its habit much resembled that of the Pacific North American *P. herrei*. More material from the North Asiatic Pacific will be required to determine whether this combination of characters is typical of another distinct, major population there, but for the present the specimen is referred to *P. interrupta*. It should be pointed out, however, that entirely typical specimens of *P. interrupta* are known from Sakhalin Island as well.

CHEMICAL ANALYSIS.—Most tests made on this species were performed by extraction of the sample in acetone without prior extraction in benzene. All samples contained atranorin and caperatic acid, which was observed in both crystal forms in the GE and GAW solutions. Fourteen of the 20 samples tested also showed a yellow pigment recrystallizing in the GE solution. This substance seems to occur in *P. erosa*, *P. formosana*, and *P. regenerans* as well. It may be a constant

component, but samples which did not give a positive test for the pigment were not retested.

The GA*o*-T solution gave yellow crystals typical of the atranorin condensation product as well as smaller finer yellow crystals (Plate 2, Figure 9). In addition, the GA*o*-T solution sometimes showed clusters of very fine colorless needles (Plate 6, Figure 36) which were not identified but which may be due to the substances producing the unidentified yellow crystals observed in the GE solution.

NOMENCLATURE.—The many references to "*Cetraria braunsiana* (Müll. Arg.) Zahlbr." in the Japanese botanical literature all relate to the present species, the result of a consistent misapplication of the name of a different plant altogether.

ADDITIONAL SPECIMENS EXAMINED:

U.S.S.R.: SAKHALIN: Ho-e, *Fujikawa*, 1932 (TNS); Kashiho, *Ishiyama*, 1932 (TNS).

JAPAN: HOKKAIDO: Prov. Hidaka: Mt. Apai, *Ikuse*, 1956 (TNS). Prov. Ishikari: Horonaizawa, *Asahina*, 1935 (TNS); Hot Spring Matsuyama, *Asahina*, 1935 (TNS); Mt. Tomuraushi, *Fujikawa*, 1935 (TNS). Prov. Kushiro: Lake Masyu, *Togashi*, 1953 (TNS).

HONSHU: Prov. Ettyu: Mt. Tate-yama, Waterfall Syo-myo, *Nishijima*, 1935 (TNS); Makawa, *Asahina*, s.d. (TNS). Prov. Izu: Mt. Amagi, *Asahina*, 1927 (TNS). Prov. Kai: Mt. Fuji, Yoshida-guichi, 1-gome, *Togashi* (TNS); the same, *Hisauchi*, 1928 (TNS); Mt. Kinpu-san, *Kurokawa* 521207 (TNS); Mt. Mizugaki, *Kurokawa* 521133 (TNS); Mt.Ko-fuji, *Asahina*, 1935 (TNS). Prov. Musashi: Pass Mikuni, *Kurokawa* 520764 (TNS). Prov. Mutsu: Mt. Osoresan, *Kurokawa* 550447 (TNS); Montagne d'Aomori, *Faurie*, 1897 (PC). Prov. Shinano: Mt. Yatsu-gatake, *Kurokawa* 520674 (TNS), *Kurokawa* 58240 (MSC); the same, Takami-ishi, *Kurokawa* 58300 (TNS); the same, Mt. Iwo-dake, *Kurokawa* 58436 (TNS); Yumatazawa, *Kurokawa* 51672 (TNS); Ikenotaira, Daimon Pass, *Asahina et al.*, 1959 (TNS); Heights Tadeshina, *Kurokawa* 58323 (TNS); Mt. Norikura, *Asahina*, 1952 (TNS, 2 collections); Mt. Daitenjo, *Kurokawa* 520518 (TNS); Mt. Gaki-dake, *Kurokawa* 520598, 520599, 520642 (TNS); Mt. Tsupakura, *Kurokawa* 520550 (TNS); Mt. Kimpu, *Asahina et al.*, 1960 (TNS); Suwa-gun, Koto-mura, Suguridaira, *Kurokawa* 58271 (TNS). Prov. Shimotsuke: Nikko, Karikomi-ko, *Culberson & Culberson* 11052, 10629 (DUKE), *Nuno*, 1961 (TNS); Nikko, Yumoto, *Nuno*, 1961 (TNS); Nikko, Yunc-ko, collector unknown (TNS, 2 collections). Prov. Suruga: Mt. Fuji, *Asahina* 72 (UPS); Mt. Fuji, between 5- and 3-gome, *Culberson & Culberson* 10655, 10662, 10669, 10757, 10806 (DUKE); Mt. Fuji, Subashiriguchi, *Asahina*, 1924 (TNS, 2 collections).

SHIKOKU: Prov. Awa: Mt. Kenzan, *Fujikawa*, 1934 (TNS), *Togashi*, 1956 (TNS). Prov. Iyo: Mt. Ishizuchi, *Fujikawa*, 1933 (TNS).

6. Platismatia lacunosa (Ach.) Culb. & Culb., comb. nov. PLATE 23

Cetraria lacunosa Ach., Method. Lich. 295. 1803. Type: North America, *Herb. Swartzii* (S, neotype).

C. lacunosa f. *cavernosa* (Menz.) Merr., Bryologist 13:26. 1910.

Lichen cavernosus Menz. *in* Ach., Lichenogr. Univ. 508. 1810 (synonym).

Platysma lacunosum (Ach.) Nyl., Bot. Not. 1855:137. 1855 (1856).

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Thallus small to large, 5–16 cm. broad; lobes 0.6–1.5 cm. broad. Upper surface gray (uniformly brown or tan in old herbarium specimens), the margins conspicuously blackening, prominently ridged by strong reticulations rising at right angles to the surface, not pseudocyphellate. Lower surface black at the center, chestnut brown at the margins, somewhat reticulately wrinkled, not punctate; rhizines few, black. Upper cortex 19–25(–29)μ thick; medulla 90–280μ thick (measurements taken between the major wrinkles), IKI –; lower cortex 13–16μ thick. Apothecia uncommon, submarginal, 0.4–2.0 cm. in diameter, expanded and irregular at maturity, apparently not perforate; hymenium 62–124μ; hypothecium and proper exciple 22–50μ thick, the limit between the two zones visible in some preparations by a somewhat differential coloration with IKI; algae in groups but usually not in a continuous layer under the proper exciple. Spores 8, ellipsoid to ovoid, 7–10×3–4.5μ. Pycnidia marginal to submarginal or even superficial (on the crests of the reticulations), the ostiole round to irregular at maturity; conidia 1×5–7μ, rod-shaped.

MEDULLARY REACTIONS.—K–, C–, KC–, PD+ orange-red.

CONSTITUENTS.—Fumarprotocetraric acid, caperatic acid (at least in some specimens), and atranorin.

DISTRIBUTION (Map, Figure 25).—The extreme west coast of North America and the coastal islands from the Aleutians and southern Alaska south to northern California; on the bark of trees (alder, hemlock, spruce) and on rock.

Although *Platismatia lacunosa* superficially somewhat resembles *P. formosana* and *P. erosa*, it can be distinguished from these and from all other species in the genus by its positive, brick-red medullary reaction with *p*-phenylenediamine due to the presence of fumarprotocetraric acid. It should not be assumed, however, that *P. lacunosa* is a mere chemical "strain" of another species; its morphological traits are quite distinct. The reticulate ridging of the upper surface that is so distinctive results from U-shaped depressions between ridges rather than the flat-bottomed spaces between thallus ridges as in the other species.

CHEMICAL ANALYSIS.—The samples were extracted with benzene at room temperature to remove atranorin, which was demonstrated in the GE and GA*o*-T solutions. The warm acetone extract of all but one of the eight samples tested contained caperatic acid (GE, GAW, and GA*o*-T). When chromatographed in pyridine-ethyl acetate-water, the acetone extracts showed fumarprotocetraric acid. Traces of other substances detected on these chromatograms could not be identified. One very faint spot with an R_f resembling that of protocetraric acid was found not to be this substance on the basis of a faint yellow fluorescence in UV light as compared to the characteristic quenching produced by protocetraric acid under the same conditions.

NOMENCLATURE.—There is a problem in the typification of this species. The Acharian Herbarium in Helsinki contains no specimens labeled *Cetraria lacunosa*. All the specimens which Acharius may have had of it, including the holotype, have apparently been lost. In Stockholm, however, there is a specimen labeled "*Cetraria lacunosa* Ach." and, written just below this but in a different hand: "Acharius scripsit" and "Herb. Swartzii." The exact history of this specimen is unknown, but there is no reason to doubt the indication that Acharius annotated it and that it was part of the herbarium of his colleague Swartz. The specimen is undated, and we do not know whether Acharius saw it before the publication of *Cetraria lacunosa* in 1803, although it is most probable that he did and that his specimen should, therefore, be considered the lectotype. In the absence of the critical historical information, however, it cannot be so designated and must be considered a neotype instead. The proper designation for type specimens selected under the conditions met with here—a common predicament in typifying many of the old names of lichens—has been discussed in detail (W. L. Culberson, 1963).

ADDITIONAL SPECIMENS EXAMINED:

U.S.A.: ALASKA: Unalaska, *Setchell et al.*, 1899 (UC), *Eyerdam*, 1932 (UC), *Hultén* 5277, 5278, 5279 (UPS); Prince William Sound, Thum Bay, Knight Island, *Eyerdam* 238, 252, 264 (UC); the same, Hinchinbrook Island, *Norberg* 328 (WIS); Port Vita, Raspberry Island, Kodiak Group, *Eyerdam* 365 (WIS); Revillagigedo Island, Ketchikan, *Eyerdam* 262 (UC); Annette Island, *Eyerdam* 497 (WIS); Admiralty Island, Windfall Harbor, *Herre* 251; Orca, *Setchell*, 1899 (UC); Attu Island, Engineers Canyon, *Hardy* 30 (S, UPS); Adak Island, Chapel Cove, *Hultén* 5875 (UPS); Atka Island, *Eyerdam*, 1932 (S), *Hultén* 5790 (UPS), *Kobayashi*, 1931 (TNS, 6 collections); Ketchikan, Deer Mountain, 1,500 ft., *Baker*, 1956 (COLO), Washington Bay, Kuiu Island, *Eyerdam* 428 (COLO), *Eyerdam* 414, 427, 509, 825 (WIS).

WASHINGTON: Grays Harbor Co.: Montesano, *Heller* 4310 (US). Jefferson Co.: Hoh River Ranger Station, *Becking* 530656 (COLO); mouth of Hoh River, *Brown & Muenscher* 154 (UC, US).

OREGON: Locality unknown, *Hall*, 1876 (US, 2 collections). Lincoln Co.: Yaguina Bay, *Hall*, 1871 (FH); Waldport, *Howard* 4628 (WIS, WTU). Marion Co.: Silverton, Powers Creek, *Foster* 1200 (US).

CALIFORNIA: Humboldt Co.: Lawrence Creek, *Park* 3512 (UC).

CANADA: BRITISH COLUMBIA: Queen Charlotte Islands, Moresby Island, 650 m., *Persson* 1957 (COLO); Vancouver Island, Comox, *Macoun* 28 (US).

7. **Platismatia norvegica** (Lynge) Culb. & Culb., comb. nov. PLATE 23

Cetraria lacunosa f. *norvegica* Lynge, Videnskaps; Skrift., Mat.-Naturv.-Kl. [Kristiania] 1921(7):196. 1921. Type: Norway, Hordaland, Store Kalsø, *Lynge*, 1920 (O, lectotype).

C. norvegica (Lynge) Du Rietz, Bot. Not. 1924:59. 1924.

C. norvegica f. *sorediata* Degel., Acta Phytogeogr. Suec. 7:52. 1935. Type: Norway, Monte Seljuåsen prope Raegefjord, *Degelius*, 1932 (not seen).

C. tuckermanii var. *sorediata* (Degel.) Räs., Kuopion Luonnon Ystäväin Yhdistyksen Julkaisuja, Sarja B. 2(6):46. 1952.

Thallus medium to large, 7–23 cm. broad; lobes 0.5–2.5 cm. broad. Upper surface gray, yellowish-gray or (especially in American specimens) distinctly yellowish, ridged, the sharp, low ridges at right angles to the surface of the thallus, pseudocyphellate, the pores generally confined to the crests of the ridges, minute, often isidiate and indistinct; isidia usually abundant along the margins of the ridges, generally associated with the pseudocyphellae. Lower surface jet-black, a marginal zone up to 1 cm. wide brown or colored like the upper surface, not punctate; rhizines black, few, usually simple. Upper cortex 19–31μ thick; medulla white, 31–217μ thick, much thicker in the ridges, IKI+ pale lavender or (apparently) IKI−; lower cortex 16–31μ thick. Apothecia rare (unknown in America), irregular, perforate, 0.7–1.5 cm. broad; hymenium 51–93μ; thick subhymenial layers measuring together 43–78μ thick, immediately underlain by a dense zone of algae. Spores 8, ellipsoid, 6–8.5×3–4μ. Pycnidia immersed, marginal; conidia not seen.

MEDULLARY REACTIONS.—K−, C−, KC−, PD−.

CONSTITUENTS.—Caperatic acid and atranorin.

DISTRIBUTION (Map, Figure 27).—Newfoundland and Miquelon Island, Canada, the western coast of North America from southern Alaska to Oregon; Norway, Sweden and southern Finland, Scotland; on rocks and the trunks of trees.

The reticulate and usually isidiate thallus of *Platismatia norvegica* is so distinctive that the species is easy to recognize. In Europe it always seems to have an adequate development of isidia, immediately distinguishing it from *P. glauca*. In western North America, however, the extent of isidia production is extremely variable, and many specimens from densely isidiate to essentially nonisidiate can be seen in herbaria, but these are marked by the same sharp, low, reticulate ridges that the isidiate plants have. This reticulation and the distinct pseudocyphellae usually associated with the ridges make these nonisidiate specimens appear quite different from *P. glauca*. *Platismatia norvegica* and *P. glauca* apparently often grow together in the Pacific Northwest as witnessed by mixtures of the species in herbarium packets. Although nonisidiate plants seem to be found only among the American populations of *P. norvegica*, the isidiate plants in the same population are indistinguishable from the European ones.

In his original description, Lynge considered this lichen species as a form of *Cetraria* (=*Platismatia*) *lacunosa*, but it differs sharply from that species both in morphology and chemistry. *Platismatia norvegica* has a pseudocyphellate, usually isidiate, minutely but sharply ridged thallus, while *P. lacunosa* has a nonpseudocyphellate, nonisidiate,

deeply reticulately ridged and pitted thallus. The medulla of *P. norvegica* is negative with *p*-phenylenediamine while that of *P. lacunosa* is brick-red.

In an occasional rare specimen of *P. norvegica* there is the development of large capitate soralia on the surface of the lobes. This modification was named *Cetraria norvegica* f. *sorediata* by Degelius. Though conspicuous, these soralia are so foreign to the scattered, granular type produced normally in the genus (as in *P. glauca* and *P. interrupta*) that they give every impression of being eruptions of the medulla through the upper cortex as the result of some external or pathological influence altogether. The occurrence of these peculiar soralia is so infrequent and their structure so bizarre that they are given no taxonomic recognition here.

Platismatia norvegica is an extremely oceanic species. It is not found beyond the area of very wet climates devoid of temperature extremes that characterize the region of the Pacific Northwest and the oceanic province of northwestern Europe. The belated recognition of the specific distinctness of this species in the well-known flora of Scandinavia prompted a number of reports and studies that ended with Ahlner's (1948) comprehensive treatment of the species in Scandinavia with a map of all collections; the reader is referred to this publication for details of the northern European range. In that paper and in Hakulinen's (1963) lichen flora of Finland, the species is also reported from extreme southern Finland. No Finnish species were seen in the present study, but we have no reason to doubt the correctness of those records.

A map of the worldwide distribution of *Cetraria norvegica* was also published by Ahlner (1948). The map in the present treatment (Figure 27) does not differ qualitatively from Ahlner's although we have added more American localities. The present study and the data collected by Ahlner (1948) also show that although the species grows on both trees and on rocks, it is more common on bark in the southern part of its range and on rocks in the northern part even though both substrate types are generally present throughout the range.

CHEMICAL ANALYSIS.—The seven samples tested contained caperatic acid and atranorin. No protolichesterinic acid was detected in the benzene extract after treatment with the GE or GAW solutions. Atranorin was proved in this extract in the GE and GA*o*-T solutions. The subsequent acetone extract contained more atranorin in addition to caperatic acid as found by treating the extract with the GE, GAW, and GA*o*-T solutions. No other fatty acids were detected. No other substances reacting with PD were found in the acetone extract after chromatography in pyridine-ethyl acetate-water (1:2:1). In the GA*o*-T solution, smaller crystals similar to the *o*-toluidine derivative of atra-

norin occurred in abundance accompanied by those of the typical atranorin derivative.

NOMENCLATURE.—Lynge listed about 30 specimens with the original diagnosis of *Cetraria lacunosa* f. *norvegica*. No type specimen was designated, but when Du Rietz elevated the forma to specific rank, he indicated as the type a Norwegian specimen collected by himself but not among those originally cited by Lynge. Since a taxon must be typified from the original material if possible, we have picked Lynge's collection from Store Kalsø in Hordaland as the lectotype. It is a large, well developed example of the species.

REPRESENTATIVE SPECIMENS EXAMINED:

CANADA: NEWFOUNDLAND: Locality unknown, *Despreaux*, 1828 (UPS); King Cove, *Dammon* 1 (US); St. John, *Fries*, 1871 (S, 2 collections).

BRITISH COLUMBIA: Queen Charlotte Islands, Graham Island, *Persson* 26, 54 (COLO); Vancouver Island, Nanaimo River Valley, *Szczawinski* 558 (US); the same, Port Renfrew, *Schneider*, s.d. (UC); the same, Comox, *Macoun* 122 (WIS).

MIQUELON ISLAND: Locality unknown, *Delamare*, 1886 (DUKE, PC), *Delamare*, as *Arn., Lich. Exs.* 1366 (PC).

U.S.A.: ALASKA: Kodiak Island, Kodiak, *Hultén* 5053 (UPS), *Eyerdam* 79 (WIS); Admiralty Island, Windfall Harbor, *Herre* 251 (UC); Glacier Bay, Beardsley Island, *Stephens* 242 (UC); Prince William Sound, Knight Island, *Eyerdam* 252, 254 (UC), *Norberg*, 1940 (S), College Fjord, *Viereck* 2419–B, Bainbridge Glacier, *Viereck* 1992–A (COLO); Kenai Peninsula, Seward, *Hultén* 7887 (UPS); Yukutat, *Schmuck* 19 (WIS); Juneau, *Hultén* 8558 (UPS).

WASHINGTON: Grays Harbor Co.: Pacific Beach, *Foster* 1359 (COLO–ABS). Jefferson Co.: Mouth of the Hoh River, *Brown & Muenscher* 154 (UC, WTU). Pacific Co.: Willapa Bay, Toka Point, *Foster* (COLO–ABS). Pierce Co.: Mt. Rainier National Park, *Pechanec* (COLO). Whatcom Co.: Mt. Baker, *Howard* 1180a (LD).

OREGON: Marion Co.: Silverton, Powers Creek, *Foster* 1200 (US).

SWEDEN: JÄMTLAND: Åre, *Ahlner*, 1951 (DUKE), *Hasselrot*, 1937 (LD), *Håkansson*, 1949 (LD), *Santesson* 48443, 48443b (UPS); Frostviken, *Stenholm*, 1918 (GB).

DALARNE: Malung, *Hasselrot*, 1934 (LD, 4 collections), *Hasselrot*, 1937 (S), *Hasselrot*, as *Magn., Lich. Sel. Scand. Exs.* 184 (GB, LD, S); Lima, *Hasselrot*, 1934 (LD).

VÄRMLAND: Munkfors, *Sundell*, 1952 (LD); Dalby, *Persson*, 1948 (S).

VÄSTERGÖTLAND: Bredareds, *Hasselrot*, 1961 (S).

NORWAY: NÖRDLAND: Elsfjord, *Ahlner*, 1939 (S); Nord-Rana, *Ahlner*, 1937 (S).

NORD-TRÖNDELAG: Egge, *Ahlner*, 1934 (S); Grong, *Österlind*, 1938 (LD); Vaerdal, *Österlind*, 1932 (LD); Sörli, *Ahlner*, 1938 (S); Malm, *Ahlner*, 1938 (S, 2 collections).

HORDALAND: Herdla, *Santesson*, 1937 (US); Voss, *Ahlner*, 1937 (S).

ROGALAND: Hjelmeland, *Degelius*, 1947 (LD); Solendal, *Hasselrot*, 1939 (S); Rege Fjord, *Hasselrot*, 1939 (US).

SOGN OG FJORDANE: Eid, *Ahlner*, 1937 (S).

SCOTLAND: Loch Rannoch, *ex herb. Stirton* (BM, 2 collections); Killin, Craig Chaillech, *M'Andrew*, 1885 (BM).

8. Platismatia regenerans Culb. & Culb., sp. nov. PLATE 24

Thallus parvus vel mediocris, 4–8 cm. latus; laciniae 0.3–1.2 cm. latae, marginibus ascendentes. Superficies superior albida vel pallide cinerea centro et marginibus nigra vel sepiacea, levis, pseudocyphellata, pseudocyphellis parvissimis et inaequalibus, corporibus parvis, regenerantibus(?), isidioideis vel complanatis in partibus vetustioribus praedita. Superficies inferior picea, marginibus castanea, vulgo reticulato-rugosa, rhizinata, fere punctata. Cortex superior prosoplectenchymatosus, 21–31μ crassus; medulla (104–)120–180(–208)μ crassa, IKI—; cortex inferior 18–26μ crassus. Pycnidia et apothecia ignota.

Thallus small to medium, 4–8 cm. broad; lobes 0.3–1.2 cm. broad, the margins ascending. Upper surface whitish or pale gray, the center and margins black or dark brown, smooth, pseudocyphellate, the pores very small and irregular, the older parts of the surface with scattered regenerative(?) bodies, isidioid or flattened and lobule-like, mostly less than 0.5 mm. broad. Lower surface black, the margins dark brown, commonly reticulately rugose, rhizinate, usually punctate. Upper cortex prosoplectenchymatous, 21–31μ thick; medulla white (104) 120–180(–208)μ thick, IKI—; lower cortex 18–26μ thick. Pycnidia and apothecia unknown.

TYPE.—Tourist Trail, just above Kambarabga radio tower, Kinabalu National Park, Sabah (Borneo), 2,000 m. alt., *Hale* 28207 (US, holotype).

MEDULLARY REACTIONS.—K—, C—, KC—, PD—.

CONSTITUENTS.—Caperatic acid and atranorin.

DISTRIBUTION (Map, Figure 29).—The high mountains of Sabah (Borneo).

The only species with which *Platismatia regenerans* might be confused is *P. erosa*. It differs from *P. erosa* in that it lacks true isidia although it may have a few flattened, apparently regenerative lobulae on the older parts of the thallus that might be mistaken for isidia.

CHEMICAL ANALYSIS.—The residue from the benzene extract of four samples tested showed atranorin in the GE and GA*o*-T solutions. These residues did not give positive tests for protolichesterinic acid in the GE or GAW solutions. The residues from subsequent acetone extractions contained more atranorin and caperatic acid. Both crystal forms of caperatic acid were observed in the GE solution, and caperatic acid was also detected in the GAW and GA*o*-T solutions. This species may also contain the unidentified substance (or substances) observed in *P. erosa*, *P. formosana*, and *P. interrupta*. One specimen showed yellow crystals in the GE solution, and another gave clusters of long fine needles in the GA*o*-T solution.

SPECIMENS EXAMINED:

SABAH (BORNEO): Kinabalu National Park, Tourist Trail, just above Kambarabga radio tower, 2,000 m., *Hale* 28207, 28932 (US); the same, woods below second radio tower (above Kambarabga), 2,200 m., *Hale* 28642 (US); the same, open ridge between East and West Mesilau Rivers, 1,800 m., *Hale* 29084 (US).

9. Platismatia stenophylla (Tuck.) Culb. & Culb., comb. nov. PLATE 24

Cetraria lacunosa b. *stenophylla* Tuck., Synops. No. Amer. Lich. 1:35. 1882.
Type: U.S.A., California, *Bolander* (FH, holotype).
Cetraria stenophylla (Tuck.) Merr., Bryologist 13:27. 1910.

Thallus medium, 5–10 cm. broad; lobes linear, narrow, (0.5)1–4 mm. broad, often becoming trough-shaped as the margins roll inwards, the margins occasionally with small lobulae oriented at right angles to the axis of the lobes, often attached to the substrate only at the base. Upper surface whitish, tan, pale brown or occasionally somewhat darkening, smooth, not pseudocyphellate, sorediate, or isidiate. Lower surface whitish, tan, or brown, not punctate, minutely reticulate-rugose, sometimes appearing veined with the crests of the ridges darkening; rhizines rare, a few at the place of attachment only. Upper cortex 16–23μ thick; medulla 86–150(–208)μ thick, IKI+ lavender; lower cortex (13–)16–21μ thick. Apothecia common, especially in the southern part of the range, terminal, 0.4–1 cm. broad, perforate or not; hymenium 39–52μ thick, subhymenium 18–34μ, thick, often underlain with algae; spores 8, small, ellipsoid or spheroid 4–5$\times$5–8μ. Pycnidia few, black, marginal; conidia 1$\times$5–8μ, rod-shaped.

MEDULLARY REACTIONS.—K−, C−, KC−, PD−.

CONSTITUENTS.—Caperatic acid and atranorin.

DISTRIBUTION (Map, Figure 23).—Western North America from Vancouver Island south to west-central California; on trees, usually near the shore.

Platismatia stenophylla is a well defined species with narrow, linear lobes, a trait shared in this genus by only *P. herrei* which is easily distinguished from the present species by its abundant marginal isidia. In the northern part of the range, *P. stenophylla* has more darkly colored thalli with strongly incurved margins and a paucity of apothecia. The southern plants are more robust, stouter, and fruit more freely. In spite of these tendencies, specimens cannot be assigned to their geographical origin with high accuracy upon habit alone, and intermediate forms are common.

Platismatia stenophylla has the most narrowly restricted geographic range of any of the American species of the genus.

CHEMICAL ANALYSIS.—The five samples tested of this species showed atranorin in the GE and GA*o*-T solutions and by chromatography. The benzene extract seemed to contain only atranorin while the subsequent acetone extract consisted of this depside mixed with caperatic

acid, which was identified by the crystals in the GE and GAW solutions. No other fatty acids were noted.

ADDITIONAL SPECIMENS EXAMINED:

CANADA: BRITISH COLUMBIA: Vancouver Island, Nanaimo Lakes, *Krajina et al.* S-15 (DUKE).

U.S.A.: WASHINGTON: Lewis Co.: Deschutes Park, Snoqualmie National Forest, *Buchta & Hedglin*, 1958 (WTU). Pierce Co.: Mt. Rainier, *Flett*, 1919 (US). Spokane Co.: Spangle, *Cooke* 23198 (WIS). Whitman Co.: Kamiak Butte, *Imshaug* 16462 (MSC).

OREGON: Benton Co.: Corvallis, *Becking* 5304666 (COLO).

IDAHO: Latah Co.: Palouse Range Ridge, *Imshaug* 16413 (MSC).

CALIFORNIA: Humboldt Co.: Locality unknown, *Bolander* (FH, US). Santa Cruz Co.: Castle Rock, *Herre* 1025, 1942, 4715 (WIS), *Herre* 3235 (COLO), *Shushan* 14737 (DUKE, US); Devils Canyon and Castle Rock, *Herre*, as *Krypt. Exs. Vidobon.* 1553 (US); Skyline Boulevard, south of Page Mill Road, *Wiggins* C-68 (DUKE); Ben Lomond, *Thiers* 9158 (WIS). San Mateo Co.: Hubbard Park, *Thiers* 9232 (WIS).

10. Platismatia tuckermanii (Oakes) Culb. & Culb., comb. nov. PLATE 25

Cetraria tuckermanii Oakes *in* Tuck., Amer. Journ. Sci. & Arts 45:48. 1843. Type: U.S.A., Massachusetts, Cambridge, *Tuckerman*, 1838 (FH, neotype).

C. lacunosa β atlantica Tuck., Proc. Amer. Acad. 1:208. 1847. Type: Lake Superior, *Agassiz* (FH, lectotype).

C. atlantica (Tuck.) Du Rietz, Bot. Not. 1925:10. 1925.

Thallus medium, to 7–12 cm. broad, loosely attached; lobes rounded, 0.4–2.2 cm. broad. Upper surface ashy-white or gray, irregularly or reticulately pitted, often conspicuously so, without pseudocyphellae, soredia, or isidia. Lower surface white or slightly tan with well defined patches becoming black or dark brown, especially toward the center of the thallus, minutely and reticulately pitted, not punctate; rhizines few, black at the center, pale or tipped with white nearer the margin. Upper cortex 18–26(–29)μ thick; medulla 109–182(–234)μ thick, the hyphae loosely interwoven, IKI –; lower cortex 16–23(–29)μ thick. Apothecia common, marginal or submarginal, 2–10 mm. broad, usually perforate; hymenium (39–)50–65(–73)μ; subhymenium 18–26 (–34)μ, IKI+ lavender, underlain by at least a few algae; spores 8, ovoid to subglobose, 4–5$\times$6–8μ. Pycnidia common, blackening, marginal or submarginal, immersed, the ostiole minute; conidia rod-shaped, ca. 1$\times$5–8μ.

MEDULLARY REACTIONS.—K –, C –, KC –, PD –.

CONSTITUENTS.—Caperatic acid and atranorin.

DISTRIBUTION (Map, Figure 31).—Southern Ontario and Quebec, Newfoundland to the Lake States and south in the Appalachians to Alabama and Georgia; on the bark of trees, primarily of conifers, and occasionally on old wooden fences.

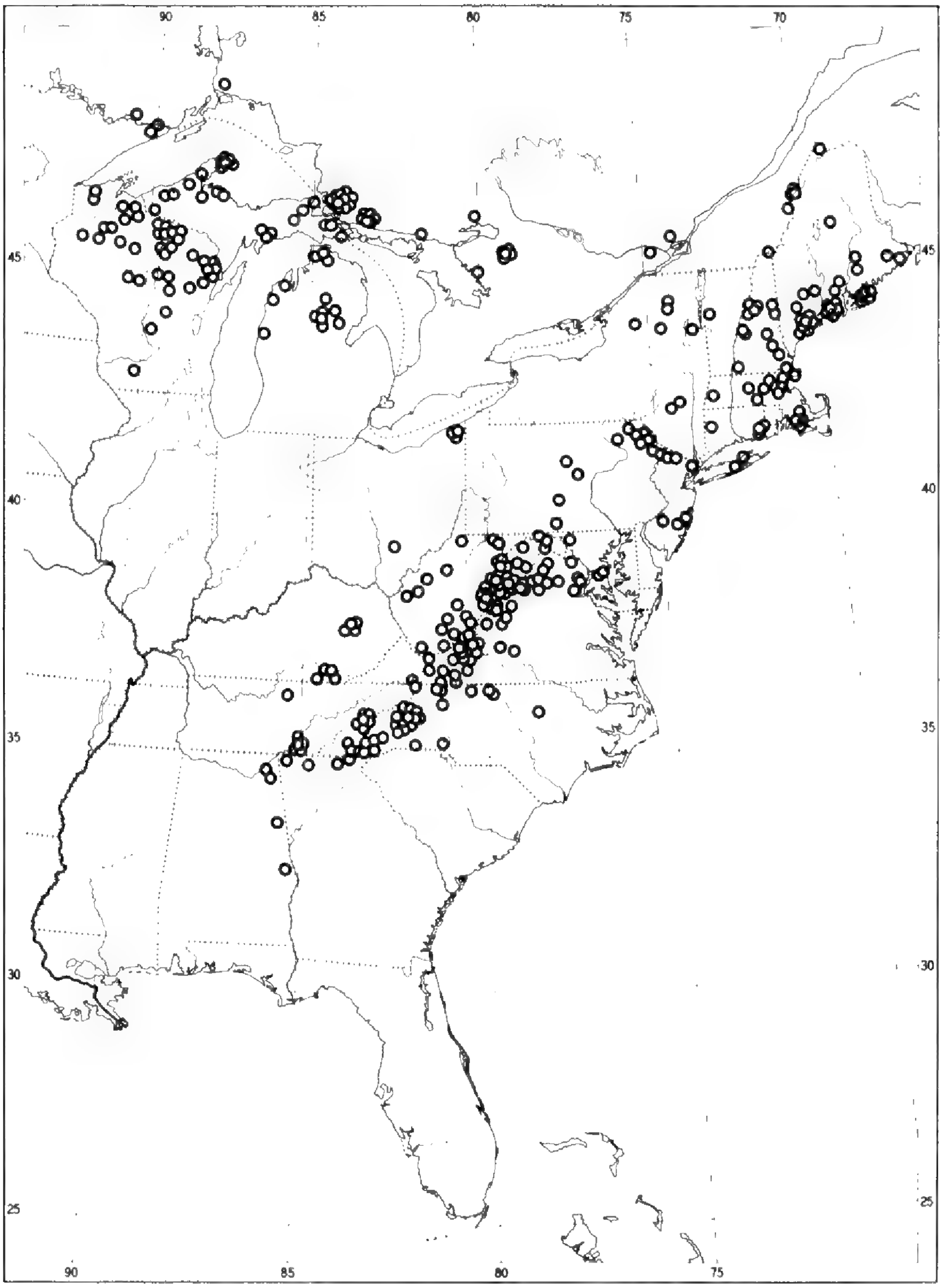

FIGURE 31. Distribution of *Platismatia tuckermanii* (Oakes) Culb. & Culb.

Platismatia tuckermanii is quite distinct from all other species. In the past it has been mistaken for *P. lacunosa* although the ranges of the species do not overlap. The thallus of *P. tuckermanii* is broadly reticulate, but it lacks the deep, sharp, thallus folds and ridges that characterize *P. lacunosa* and differs chemically in lacking fumar-

protocetraric acid and therefore reacts negatively with *p*-phenylenediamine.

In herbarium collections, members of the *Cetraria ciliaris* Ach. and related species have often been mistakenly identified as *Platismatia tuckermanii*, doubtless because these plants regularly grow together throughout their range. The members of the *Cetraria ciliaris* group all have marginal stalked pycnidia, usually have marginal cilia, and the most common species have aromatic constituents (alectoronic, α-collatolic, olivetoric, and physodic acids) which give positive reactions with C or KC. *Platismatia tuckermanii* lacks all of these traits. There are also fundamental differences in the anatomy of the upper cortex between the species.

Platismatia tuckermanii is also sometimes mistaken for *P. glauca* although almost invariably it is the more abundant of the two species in places where they grow together. It can be differentiated at once from esorediate and nonisidiate specimens of *P. glauca* by its negative thallus reaction with IKI which in *P. glauca* is strongly positive, producing a deep blue-black coloration. Although many morphologic characters separate the two species, the IKI test is quickly used and definitive.

Platismatia tuckermanii is broadly distributed in northeastern temperate North America. The species belongs to the northern conifer-dominated forests and becomes rare abruptly outside of this vegetational region.

Platismatia tuckermanii shows a strong preference for the bark of coniferous trees. In northern Wisconsin where the species is common, its presence at breast height in quadrats on 2,000 randomly selected trees was analyzed (Culberson, 1955). It was found on 19 percent of the white pines (*Pinus strobus*), 7 percent of the jack pines (*Pinus banksiana*), 2 percent of the lindens (*Tilia americana*), and about 1 percent of the red pines (*Pinus resinosa*), hemlocks (*Tsuga canadensis*), red oaks (*Quercus rubra*), yellow birches (*Betula lutea*), and sugar maples (*Acer saccharum*). It was absent from the white birches (*Betula papyrifera*), red maples (*Acer rubrum*), beeches (*Fagus grandifolia*), and poplars (*Populus* spp.). Elsewhere in its range its preference for coniferous trees is also obvious. It is also sometimes found on old wooden fences but almost never on rocks.

CHEMICAL ANALYSIS.—Seven samples were tested and all contained atranorin as demonstrated in the GE and in GA*o*-T (Plate 2, Figures 8 and 10) solutions. The benzene extract gave no crystals of protolichesterinic acid in the GE or GAW solutions, but the subsequent acetone extract showed caperatic acid. Crystals of caperatic acid were observed in the GE (in both crystal forms), GAW, and GA*o*-T solu-

tions. The acetone extract chromatographed in pyridine-ethyl acetate-water showed no components reacting with PD other than atranorin.

NOMENCLATURE.—No specific collections were cited with the description of *Cetraria tuckermanii* Oakes and no original collections of undisputed authenticity exist. The neotype selected here (see above) is a specimen in Tuckerman's herbarium (FH) bearing the name "*Cetraria tuckermanii*" and collected in Massachusetts five years before Oakes' description was published. There is no doubt of the reference intended in the application of Oakes' name, and the neotype fits the description well. It is also highly probable that Oakes even examined this very collection when he described the new species.

In his description of *Cetraria lacunosa β atlantica*, Tuckerman cited two specimens, one from New York and the other from Pennsylvania. Today there are no specimens labeled with this name in his herbarium. In the original description the range is given as "Lake Superior to New England." In Tuckerman's herbarium there is a specimen collected by Agassiz and labeled "Lake Superior." This collection, from Louis Agassiz's famous trip, is undoubtedly the material upon which the statement concerning the geographic range in the original description referred. We designate this specimen as the lectotype of *C. lacunosa β atlantica*.

Du Rietz (1925) cited specimen number 468 in *Reliquiae Farlowianae* as the type of *C. lacunosa β atlantica*, but this undated New Hampshire collection, issued simply as *C. lacunosa*, cannot in any way be associated with the original diagnosis of the variety.

REPRESENTATIVE SPECIMENS EXAMINED:

CANADA. ONTARIO: Algoma District, Mississagi River, *Cain* 25867, 25870, 25872 (US), Timagami, Gull Lake, *Cain* 26782 (COLO, US); Emo, *Fink* 739 (K, MSC, UC); Ottawa, *Couet* 1899 (PC).

QUEBEC: Bellechasse Co.: Ste. Camille, *Masson* 5007, 5008, 6182, (WIS). Terrebonne Co.: Parc du Mont Tremblant, *Hermann* 15759 (US). Woburn Co.: Frontenac, *Masson* 6031 (WIS).

U.S.A.: MAINE: Hancock Co.: Mt. Desert Island, *Tuckerman*, 1871 (FH). Lincoln Co.: Hog Island, *Wiley*, 1953 (WIS). Piscataquis Co.: Mt. Katahdin, *Degelius*, 1939 (US). Washington Co.: North Lubec, *Cummings, Dec. North Amer. Lich.* 279 (DUKE, WIS).

VERMONT: Addison Co.: Bristol, *Faxon*, 1879 (WIS).

NEW HAMPSHIRE: Belknap Co.: Gilmanton, *Blake* 5 (COLO). Carroll Co.: Chocorua, *Farlow, Rel. Farlowianae* 468 (UC, US, WIS). Grafton Co.: North Woodstock, *Cummings, Dec. North Amer. Lich.* 46 (DUKE, MSC, US, WIS).

MASSACHUSETTS: Bristol Co.: New Bedford, *Willey* 109 (US). Essex Co.: Manchester, *Seymour*, 1908 (UC). Worcester Co.: Lunenburg, *Sargent*, 1883 (UC).

CONNECTICUT: New London Co.: Norwich, *Setchell*, 1883 (UC).

NEW YORK: Essex Co.: Chilson Lake, *Harris*, 1898 (COLO–ABS, US). Greene Co.: Maplehurst, *Dix*, 1929 (DUKE). Suffolk Co.: Riverhead, *Brodo* 1097 (MSC).

NEW JERSEY: Bergen Co.: Closter, *Grout* 6185 (DUKE). Burlington Co.: Chats-

worth, *Darrow* 1905 (WIS). Ocean Co.: Lakehurst, *Thomson*, 1940 (WIS). Sussex Co.: Highview Mountain State Park, *Hale* 17291 (DUKE, US).

PENNSYLVANIA: Clinton Co.: Westport, *Hale* 16082 (US). Huntingdon Co.: Penn State Nature Camp, *Thomson*, 1937 (WIS). Monroe Co.: Pocono Pines, *Kaiser*, 1910 (DUKE). Susquehanna Co.: Starruca Station, *Dix*, 1940 (DUKE). Wayne Co.: Scott Center, *Dix*, 1941, 1943 (DUKE, 2 collections).

OHIO: Ashtabula Co.: Orwell, *Bogue* 269 (DUKE). Hocking Co.: Old Man's Cave, *Hale* 13328 (US).

KENTUCKY: Lee Co.: Beattyville, *Hale* 13758 (US). Menifee Co.: 10 mi. southwest of Mariba, *Hale* 13423 (US). Powell Co.: Natural Bridge State Park, *Braun*, 1916 (DUKE). Whitley Co.: Cumberland Falls, *Hale* 13105 (US).

WEST VIRGINIA: Cabella Co.: Milton, *Hale* 10779 (US). Gilmer Co.: Cedarville, *Hale* 10500 (US). Hardy Co.: Mathias, *Gillespie* 15437 (US). Monroe Co.: Peterstown, *Hale* 13064 (US). Pendleton Co.: Judy Gap, *Hale* 10127 (US). Pocahontas Co.: Michael Mountain, *Gray* 3254, (COLO–ABS). Raleigh Co.: Clear Creek, *Hale* 11840 (US). Tucker Co.: Canaan Mountain, *Allard* 10907A (US).

VIRGINIA: Appomattox Co.: Appomattox Surrender Grounds, *Hale* 15610 (US). Culpeper Co.: Jeffersonton, *Hale* 18472 (US). Giles Co.: Mountain Lake, *Culberson* 11251 (DUKE). Grayson Co.: Comers Rock, *Hale, Lich. Amer. Exs.* 60 (COLO, DUKE, MSC, UC, WIS). Page Co.: Shenandoah National Park, *Ireland* 3776 (US). Smyth Co.: Whitetop Mountain, *Hale* 18629 (US). Wythe Co.: Wytheville, *Hale* 12024 (US).

MARYLAND: Anne Arundel Co.: Locality unknown, *Tuckerman*, 1852 (FH). Prince Georges Co.: Cedarville State Forest, *Hale* 14346 (US).

NORTH CAROLINA: Avery Co.: Grandfather Mountain, *Moore* 1897 (DUKE). Gaston Co.: Gastonia, *Culberson* 5258 (DUKE). Jackson Co.: Glenville, *Culberson* 5748 (DUKE). McDowell Co.: Buckcreek Gap, *Culberson* 4873 (DUKE).Macon Co.: Mt. Staula, *Moore* 1592 (DUKE). Mitchell Co.: Spruce Pine, *Culberson* 4847 (DUKE). Orange Co.: Hillsborough, *Culberson* 12069 (DUKE). Yancey Co.: Mt. Mitchell, *Culberson* 4814 (DUKE).

TENNESSEE: Hamilton Co.: Lookout Mountain, *Calkins* 236 (UC). Johnson Co.: Backbone Rock Recreational Area, *Hale* 18408 (US). Sevier Co.: Mt. Le Conte, *Degelius*, 1939 (US).

SOUTH CAROLINA: Greenville Co.: Greenville, *Hale* 7759 (US).

GEORGIA: Dade Co.: Trenton, *Hale* 7383 (US). Murray Co.: Chatsworth, *Hale* 7423 (US). Towns Co.: Hiwassee, *Culberson* 7274 (COLO, DUKE, US). Union Co.: Vogel State Park, *Hale* 7343 (US).

ALABAMA: Cleburne Co.: Cheaha Park, *Hale* 7113 (US). De Kalb Co.: De Soto Park, *Hale* 7024 (US). Jackson Co.: Section, *Hubricht* B2182 (WIS). Lee Co.: Auburn, *Becking* 5910004 (US).

MICHIGAN: Baraga Co.: Covington, *Imshaug* 20846 (MSC). Chippewa Co.: Hulbert, *Thomson* 1008 (WIS). Houghton Co.: Rice Lake, *Wetmore* 1315 (MSC). Keweenaw Co.: Isle Royale, *Wetmore* 2522 (COLO, WIS). Marquette Co.: Cliff Lake, *Imshaug* 4325 (WIS). Schoolcraft Co.: Big Spring Indian Lake, *Imshaug* 19993 (MSC).

WISCONSIN: Adams Co.: Friendship, *Culberson* 3120 (WIS). Ashland Co.: Mellen, Lake Galilee, *Culberson* 3629 (WIS). Door Co.: Porte des Morts Strait, *Culberson* 4145 (WIS). Douglas Co.: Brule River Valley, *Thomson, Lich. Wiscon. Exs.* 39 (COLO, DUKE, MSC, WIS). Iron Co.: 16 mi. south of Hurley, *Culberson* 3125 (MSC, WIS). Taylor Co.: Rib Lake, *Culberson* 4235 (WIS). Oneida Co.: Woodruff, *Thomson, Lich. Wiscon. Exs.* 18 (COLO, DUKE, MSC, US, WIS). Vilas Co.: Lac Vieux Desert, *Cheney*, 1893 (WIS).

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